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GAMETOGENESIS AND FERTILIZATION IN ALBUGO.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX.

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(WITH PLATES I–IV)

BEFORE the publication of my paper (1899) describing the fertilization of *Albugo Bliti*, the mature oosphere in the Phycomycetes was generally conceded to be a uninucleate structure. The question of homologies in the group did not then seem difficult. *A. Bliti*, however, presented a unique condition, in that about one hundred antheridial nuclei fuse in pairs with an equal number of egg nuclei. This condition seemed remarkable and inexplicable, inasmuch as Wager (1896) had studied the fertilization in *A. candida*, and had described a fusion of single male and female nuclei in a uninucleate oosphere. Such divergence in the same genus led to some speculation. Davis (1900) reexamined *A. candida* and fully confirmed Wager's account, as indeed Berlese (1898) had already done. It is well established, therefore, that there is a simple fusion in *A. candida*, and my own account (1899) stands for a multiple fusion in *A. Bliti*. Interest also attaches to this genus on account of the presence of a coenocentrum, a structure of prominence, but of hitherto unknown function.

The study of *A. Portulacae* and *A. Tragopogonis* was undertaken in the hope that these species might help to explain the

apparent discrepancy between the two species previously studied. The selection of *A. Tragopogonis* has proved particularly fortunate, for it has led directly to a solution of the problem. The conditions in this species, while to a certain extent similar to those described for *A. candida*, made evident the necessity of a critical reexamination of the latter. I have included *A. candida*, therefore, in this investigation.

The material of *A. Portulacae* on *Portulaca oleracea*, and *A. Tragopogonis* on cultivated *Tragopogon* and *Ambrosia artemisaefolia*, was collected at Syracuse, New York. The material of *A. candida* on *Bursa* was collected at Columbus, Ohio. All the material was fixed in chrom-acetic killing fluid and imbedded in paraffin in the usual way. The methods in general were the same as those employed in the study of *A. Bliti*, and are described in detail in BOT. GAZ. **28**: 233. 1899. The Flemming triple stain was used throughout, and I am convinced that it is best for the study of Albugo, although it is exceedingly sensitive to manipulation, and the different species of Albugo require quite different treatment.

The results of this investigation are presented in three sections, entitled "descriptive," "phylogeny," and "general considerations." The first section describes the phenomena observed, avoiding theoretical considerations and presenting only what may be regarded as established facts. The second section considers the phylogenetic bearing of this research. The third section considers the genus from the comparative standpoint, an attempt being made to interpret the significance of the phenomena, and to call attention to analogous phenomena in other organisms.

The species discussed were kindly determined by Dr. Paul Magnus, who assures me that the names and synonymy are as follows: ALBUGO PORTULACAE (DC.) O. Ktz. (*Uredo Portulacae* DC., *Cystopus Portulacae* Lév.); A. TRAGOPOGONIS (Pers.) S. F. Gray (*Uredo candidus Tragopogonis* Pers., *Cystopus Tragopogonis* Schröt., *Uredo Tragopogonis* DC., *Cystopus cubicus* Lév., *C. spinulosus* DBy., *Uredo cubica* Strauss); A. CANDIDA (Pers.) O. Ktz. (*Uredo candidus* Pers.).

I wish to express my chief thanks to Professor Strasburger for daily counsel during the progress of this research; to Professor Magnus for names and synonymy; to my wife for the preparation of the slides, and for Plate IV; and to the University of Chicago for the advantages derived from a traveling fellowship.

I. DESCRIPTIVE.

ALBUGO PORTULACAE.

The early stages of the sex organs in *A. Portulacae* differ in no essential detail from those described for *A. Bliti* (Stevens 1899, *figs. 42, 43, 45, 59–65*). The nuclei are distorted as the protoplasm flows into the developing oogonium, but as this structure attains its full growth and recovers its turgor they regain their spherical form and enlarge, rapidly assuming the spirem condition. They are more numerous than in any of the other species examined, ranging from 300 to 400 in each oogonium, and are smaller than in *A. Bliti*, rendering this an unfavorable type for cytological study.

The aggregation of the cytoplasm into several regions of greater density is the first indication of the development of the oosphere (*fig. 1*). The aggregations soon coalesce, forming one large mass of fine uniform cytoplasm. Apart from the structural differences between the dense alveolar center and the vacuolate filar periphery, there is a very distinct difference in stain reaction. The dense fine-grained cytoplasm refuses the gentian, but takes the orange G lightly, while the vacuolate peripheral cytoplasm takes the gentian strongly. The uniform dense alveolar region is the rudimentary oosphere, and is centrally placed in the oogonium (*fig. 3*).

Throughout this differentiating process the nuclei, which are now in mitosis, are crowded out of the denser masses and come to lie near the larger vacuoles (*fig. 2*). Therefore, after the denser masses have coalesced and the larger vacuoles are forced into the periplasm, the nuclei are to be found near the rather indefinite boundary between periplasm and ooplasm. This boundary, however, becomes distinct and sharp immediately

after the nuclei have passed to the periphery. Meanwhile the mitosis advances from prophase to metaphase.

The oogonium in this condition presents typically a region of uniform finely vacuolate cytoplasm devoid of nuclei, surrounded by a zone of cytoplasm bearing large vacuoles and containing the nuclei in metaphase. This condition I have termed the stage of *zonation* (*fig. 3*). A full understanding of this stage is necessary to interpret it in other species. Zonation presents the first clear differentiation of ooplasm from periplasm at a time previous to the existence of any wall between these parts, and finds the ooplasm nearly or quite devoid of nuclei. Zonation is very definitely and clearly marked in *A. Bliti* and *A. Portulacae*, the periplasm and ooplasm being as sharply separated as though an actual wall existed between them, but is much less conspicuous in *A. Tragopogonis* and *A. candida*, thus rendering these species more difficult of interpretation.

Immediately following zonation the nuclei divide, many of them lying in such a position that one of their daughter nuclei reenters the ooplasm. In *A. Bliti* nuclei are frequently found in late anaphase with one daughter nucleus lying inside of the oosphere and the other in the periplasm, thus affording direct evidence of the derivation of the primary oospheric nuclei. This rarely occurs in *A. Portulacae*, as the dividing nuclei usually lie quite outside of the line separating ooplasm and periplasm. The results, however, are precisely those presented in *A. Bliti*, namely, one of the daughter nuclei of each mitotic figure, lying with its long axis approximately perpendicular to the boundary of the oosphere, reenters the ooplasm (*figs. 4, 5*). The resulting oosphere contains many nuclei, the number usually varying from 50 to 100 in this species.

These primary oospheric nuclei now divide mitotically, and their products function as the female sexual elements. It should be carefully noted that there are here, as in *A. Bliti*, two mitoses in the oogonium. The first occurs during the differentiation of the oosphere and provides the primary oospheric nuclei. The second occurs in the oosphere (*figs. 6, 7*) and results in the

female nuclei. These two divisions may be recognized at a glance, inasmuch as the mitoses are simultaneous for all the nuclei concerned. The nuclear figure of the second mitosis differs from that of the first in that the nuclear membrane disappears and there are fewer spindle fibers. The second mitosis usually affects only those nuclei that lie in the clearly differentiated oosphere.

Peculiar activities are present in the center of the oogonium shortly before zonation, which lead to the formation of the coenocentrum. This structure, much less conspicuous and much more ephemeral in *A. Portulacae* than in *A. Bliti*, is of the same general nature, however, and needs no special description. The central globule is found only rarely and is very small.

The development of the antheridium of *A. Portulacae* is similar to that of *A. Bliti* in its general features. Simultaneously with the mitosis of the oogonium two mitotic divisions occur in the antheridium, but the difference which is so clearly apparent between the nuclear figures of the first and second mitoses in the oogonium is not found in the antheridium. The antheridial cytoplasm stains darkly with the gentian violet, and resembles the periplasm rather than the ooplasm of the oogonium. The antheridia lie closely appressed to the oogonia, and it is not unusual to find more than one adhering to the same oogonium, a condition much more rarely seen in *A. Bliti*.

A slight papilla is developed from the oogonium into the antheridium at their point of contact. This is the "receptive papilla," first described by Wager (1896) for *A. candida*, and it reaches most remarkable proportions in *A. Portulacae* (*figs. 1, 5, 6*). In its early stages it resembles the receptive papilla of *A. candida* and *A. Bliti*, being merely a slight protuberance extending from the oogonium to the antheridium.[1] In *A. Portulacae*, however, it reaches much greater proportions (*fig. 5*). Its development occurs at a later period than in the other species, usually after the differentiation of the oosphere or even during

[1] The account of the structure in *A. Bliti* (Stevens 1899) traces the growth of the papilla in detail.

the second mitosis, while in *A. Bliti* it precedes the preliminary massing of the cytoplasm. In *A. Portulacae* the oosphere sometimes protrudes into this papilla, a phenomenon not occurring in *A. Bliti*, since its oosphere has not been differentiated when the papilla is formed. The condition presented in *fig. 6* shows that sometimes the papilla becomes ruptured. This I cannot regard as normal, however, since only one of the hundreds of preparations examined shows such a condition.

The mode of formation of the antheridial tube is uncertain. In somewhat advanced stages it is found extending nearly to the center of the oosphere. It has a well-defined wall, and is firm and straight (*fig. 8*), differing from the swollen gelatinous tube of *A. Tragopogonis* and *A. candida*, but agreeing closely with that of *A. Bliti*.

In no case was the antheridial tube in a mature oogonium seen to contain less than fifteen nuclei, and in most cases there are probably 150 or more. I have seen the tubes in transverse, longitudinal, and oblique sections, and they were always multinucleate and extended into multinucleate oospheres (*figs. 7–9*). The male nuclei are oval as they lie in the end of the antheridial tube, and stain more darkly at the anterior end. Whether there is any constant numerical relation between the sperm nuclei and oospheric nuclei could not be determined with any accuracy, owing to the great number of sperm nuclei crowded into the antheridial tube. When fully developed, the antheridial tube opens as in *A. Bliti*. There is first a softening of the wall, which is probably due to the presence of an enzyme, and it is finally dissolved, allowing the nuclei to escape and pair with those of the oosphere (*figs. 10, 11*). Before fusion both male and female nuclei enlarge somewhat, although they maintain a typical resting condition during fusion and regain their original size soon after. The result is an oospore containing between 100 and 200 nuclei, which passes the winter without further change.

A very few winter spores were seen with a relatively small number of nuclei, in one case as few as six, but this condition must be regarded as very exceptional. Such cases probably

result from a fertilization of oospheres containing few female nuclei, and such are rare.

It is unnecessary to describe further the development of the spore, since its course is apparently parallel with that of *A. Bliti*. It consists simply of an accumulation of food stuffs and a growth of protective structures. A portion of a mature wall is shown in *fig. 12*. The endospore consists of one layer only, not two, as I have described in *A. Bliti*.

Berlese, in a recent paper, entitled "Ueber die Befruchtung und Entwickelung der Oosphäre bei den Peronosporeen," discusses some of the cytological phenomena of this genus. In this study he has included observations on *A. Portulacae*, giving six figures to represent the species. His results differ essentially from mine, a difference which is the more interesting since similar technique was employed, and in both cases the host plant was *Portulaca oleracea*. For the sake of clearness I will indicate some of the discrepancies between his work and my own. Berlese finds thirty to forty nuclei in an oogonium before mitosis, and says that these nuclei divide several times, the nucleoli vanishing during prophase. My preparations show 300 to 400 nuclei which divide twice, their nucleoli persisting till late anaphase. He finds ten to twelve nuclei in an antheridium, while my material shows a number several times greater. Notwithstanding his statement (p. 176), "das Cytoplasma, welches den in der Gonosphäre zurückgebliebenen Kern umgiebt, ist dicht und sehr fein gekörnt," the ooplasm which he represents is much more coarsely vacuolate (Berlese, 1898, *figs. 2–4*) than in any Albugo I have examined. Indeed, it does not resemble the ooplasm of a typical Albugo, which varies but little, so far as my observation goes, but rather presents the features of the ooplasm of Peronospora. He notes no "receptive papilla," and the antheridial tube in both stfucture and content is very unlike that described in this paper. He describes the chromosomes as visible in the male nucleus during fusion (p. 179), and counts them. None of the species I have examined presents a possibility of counting chromosomes at this stage, inasmuch as the

nuclei fuse in typical resting condition, and the chromosomes are then absolutely indistinguishable. Many other discrepancies might be enumerated.

Such marked divergences, aside from the fact that Berlese has described a uninucleate oosphere and antheridial tube, while I find them both clearly multinucleate, are sufficient to warrant the suspicion that we are working with quite different species. Still, only one species is as yet described on *Portulaca oleracea*, and the configuration of the spore wall represented and described by Berlese agrees fully with that of the form discussed in this paper.

I have taken particular care to convince myself of the identity of the species used, and have the assurance of Professor Magnus that my species is truly *Albugo Portulacae*. Furthermore, I have been able to compare this material with authentic European herbarium specimens, and they agree precisely. Not only do my preparations agree with European material in gross characters, but the cytoplasmic structures agree with those carefully figured by Istvánffi (1895, *pl. 36, figs. 24, 25*). This agreement emphasizes the identity of the American with the European species, and further shows that the species from widely separated regions[2] do not vary appreciably even in the cytoplasmic phenomena regarding which Berlese and I report such diametrically opposed observations.

It is difficult to explain these numerous and serious discrepancies. Great variation in cytological detail is to be expected in this genus, and possibly the Italian form differs from the American as well as from that which Istvánffi studied. This is improbable, however, in view of the close agreement between these two latter forms. The problem can hardly find definite solution until the Italian form has been studied more closely. A mere difference in the number of functional nuclei, even a difference so great as that between the multinucleate and uninucleate oosphere, is readily conceivable in the same species when

[2] I have been unable to learn where Istvánffi collected his material, but assume that it is of European origin.

the condition presented by *A. Tragopogonis* is borne in mind. Berlese, however, describes no such phenomena as are seen in *A. Tragopogonis*, nor does he see the coenocentrum. Thus it appears that in the Italian form the reduction to a uninucleate condition, if such a condition really exists, is of an entirely different nature from that described in this paper.

ALBUGO TRAGOPOGONIS.

In *A. Tragopogonis* there is a simple fertilization. One male nucleus is conveyed into the oosphere, where it fuses with one oospheric nucleus. To understand the variation between this form of fertilization, also characteristic of *A. candida*, and that shown by *A. Bliti* and *A. Portulacae*, it is necessary to follow carefully the stages in the development of the oosphere in the two former species, and to homologize them with those presented by the two latter.

In *A. Tragopogonis* the oogonium and oospore are smaller than in *A. Bliti* or in *A. Portulacae*. The number of nuclei is less in proportion to the size of the oogonium, however, so that for each nucleus there is more available space. This obviates much of the dense crowding of mitotic figures seen in *A. Bliti* and in *A. Portulacae* at the time of zonation, rendering this a favorable type for study. The small size of the oosphere, however, makes it much more difficult to recognize the stages of development, so that even the preliminary examination must be made under an immersion lens.

The early stages are similar to those described for *A. Portulacae*. The protoplasm flows into the oogonium, the nuclei enlarge, the cytoplasm masses in the center, and finally the fully developed stage of zonation is reached. As in *A. Bliti* and *A. Portulacae*, this is a well-marked developmental stage (compare *figs. 28* and *3*), although it does not stand out with quite the clearness that obtains in those species. There is one central area of dense fine-meshed alveolar ooplasm, which is very clearly differentiated from the filar deeply staining periplasm. The central region, which at this time contains a very prominent

coenocentrum, is entirely devoid of nuclei. They surround the central region, lying wholly within the periplasm, and are usually in metaphase. In this species, as in *A. Portulacae*, the mitosis is nearly completed in the periplasm, and the daughter nuclei do not begin to push back into the ooplasm until the chromosomes have retreated from the equatorial region of the spindle. It is also apparent that only those nuclear figures which are appropriately oriented contribute daughter nuclei to the ooplasm, and that only one of the pair gains entrance. From their mode of entrance it follows, as in *A. Portulacae*, that the chromatic content of the nuclei is situated at the end most distant from the sister nucleus. The nuclei number about fifty, and the tendency toward lowering the number that is occasionally seen in *A. Portulacae* is not apparent here.

The primary oospheric nuclei now undergo a second mitosis, which is clearly distinguishable from the first by the character of the chromatic figure, which is similar to that described for *A. Portulacae*. The fact that the second mitosis involves only the oospheric, not the periplasmic nuclei also distinguishes it from the first (*figs. 32, 34*).

The definiteness with which ooplasm and periplasm are delimited at and after zonation (*figs. 28–31*) precludes any possibility of confounding pre- and post-zonation stages. The clearness of the nuclei, which are seen as they enter the oosphere (*fig. 29*), and which can be followed through all the stages of the second mitosis (*figs. 32, 34*), renders it equally certain that in *A. Tragopogonis* the oosphere is multinucleate. So far there has been no deviation from the course followed by *A. Bliti* and *A. Portulacae*.

These potential female nuclei appear to differ from each other in no important respect, unless it be in their distance from the coenocentrum, yet under the usual conditions only one of them is destined to function as a sexual nucleus. A study of later stages shows that one (or very rarely two or three) of these nuclei comes to lie in close contact with the coenocentrum, and there grows (*figs. 35–37*) until it becomes many times its former

size and much larger than the nuclei found at earlier stages in the developing oosphere.

A study of oospheres after the second division shows the potential female nuclei in various stages of degeneration. They appear first to lose their chromatin network, the nucleoli and membrane persisting longest. Such degenerate nuclei can be found in abundance in the stages indicated. Frequently one or two rather large and apparently normal nuclei are found in an oosphere, which also has its one large nucleus in contact with the coenocentrum. In other cases, many very small nuclei are to be found in the ooplasm, and one large nucleus near the coenocentrum. These small nuclei range from the normal size to such small dimensions that only the nucleolus can be perceived with certainty. It would be impossible to recognize the smallest as nuclei, were it not that they are connected with undoubted nuclei by a series of complete gradations, and from the fact also that they lie in a cytoplasm remarkably clear and free from granules. Occasionally these extremely small nuclei are found in mitosis. Sometimes I have found groups of supernumerary nuclei, and often small ones are found in pairs, as though trying to fuse (*fig. 38*). Since this condition has never been found before the opening of the antheridial tube, it may represent the pairing of a supernumerary oospheric with a degenerate antheridial nucleus.

That these inclusions described as degenerate nuclei are really nuclei is established by their structure and behavior. That they do not result from the division of a fusion nucleus is shown by their presence when the male and female nuclei are found lying together, but still unfused in the same oosphere (*fig. 38*). The degenerate nuclei, as would be expected, are most numerous immediately after the second mitosis, while the one functional nucleus which lies near the coenocentrum is yet small. Before the opening of the antheridial tube nearly all have disappeared. There is convincing evidence that the oosphere is at first multinucleate (*figs. 30–32, 34*) and eventually uninucleate (*fig. 36*). There is no evidence to indicate

that any nuclei escape through the boundary into the periplasm, but they are seen in the ooplasm in all stages of degeneration.

The coenocentrum in *A. Tragopogonis*, as in *A. Bliti* and *A. Portulacae*, makes its appearance when the central mass of ooplasm is formed just before zonation (*figs. 27, 28*). It first consists of an area of cytoplasm which takes the orange G with great avidity, while the neighboring cytoplasm stains deeply with the gentian violet. A trifle later than zonation the coenocentrum is very highly developed, and appears in section as several zones of cytoplasm differing in density and stain reaction. The innermost area is coarsely vacuolate, and stains lightly with orange G. This region is surrounded by a narrower zone of dense granular cytoplasm, which is in turn encompassed by a less dense zone, and this finally by a broad zone of cytoplasm which stains more deeply with gentian violet. This condition is not greatly changed at the time of entrance of the primary oospheric nuclei represented in *fig. 30*. In later stages the outer zones are lost, and the innermost region assumes a characteristic homogeneous oily appearance and is quite spherical (*fig. 31*). About the time of the second mitosis the innermost region, all that remains of the coenocentrum, loses its clear appearance and becomes coarsely granular (*fig. 32*), and in its stain reaction shows the probability of nuclear contents. The vacuolate area seen in the center of very young coenocentra (*fig. 30*) is probably a reservoir for the reception of foods that are elaborated by the surrounding (presumably zymogenic) zone, which is in turn encompassed by typical trophoplasm. As the coenocentrum becomes older, these vacuoles, or rather globules of food stuffs in the protoplasm coalesce, and form the one central globule, which at first has a clear oily appearance (*fig. 31*), although it is not a true oil.

The coenocentrum possesses an attraction for the nuclei similar to that noted by Wager (1900) in *Peronospora parasitica*. Nuclei in greatly elongated condition, apparently moving toward the coenocentrum, give sufficient evidence of this (*figs. 30, 31*). As a result, several nuclei come into actual contact

with and even penetrate the coenocentrum (*figs. 32, 34*), and are thus found during all stages of the second mitosis. In some cases only one nucleus in mitosis is found thus attached; in others as many as three seemed to be so anchored, and probably, if the sphere could be viewed from all sides, as many as six or seven nuclei could be seen attached to the coenocentrum. The other primary oospheric nuclei are found lying free in the neighboring ooplasm in a similar stage of mitosis. It is not probable that any nuclei actually enter the coenocentrum, inasmuch as it maintains its homogeneous appearance until considerably later.

After the completion of the second mitosis, one small nucleus is found lying very close to the coenocentrum, possibly attached to it, although the evidence in *A. Tragopogonis* is not clear. Older stages show a larger nucleus. As the size of the nucleus increases, the coenocentrum becomes more granular (*figs. 35–37*), and loses its definite form, eventually appearing simply as a granular mass partially enveloping the female nucleus. As has been said, there is usually only one nucleus lying beside the coenocentrum after the completion of the second division, although several are in contact with it during this process. The oosphere when ready for fertilization contains one large nucleus which lies beside the remains of the coenocentrum. A few small degenerating nuclei, frequently present, are scattered throughout the ooplasm, which still maintains that fine-meshed alveolar structure that characterizes it after zonation.

Few phenomena of interest were observed in connection with the entrance of the antheridial tube. It has a much thinner wall, and is of more gelatinous nature, than that of *A. Bliti* or of *A. Portulacae*, and disappears more quickly after discharging its contents. It usually bears several degenerate nuclei as well as one or two that are larger and apparently capable of functioning. *Fig. 33* shows an unopened tube which contains a greater number, although in this case the oosphere clearly possessed only one functional nucleus. The rupture of the tube, accompanied

by the discharge of its contents, may occur at some distance from the female nucleus or nearly in contact with it. When the sperm nucleus is liberated it assumes an oval shape as it migrates toward the female (*fig. 36*).

The male is much the smaller when the nuclei first come in contact, although at this time it is larger than an ordinary vegetative nucleus. Fusion does not occur at once, but the nuclei lie together, imbedded in the remains of the coenocentrum. This period of rest must be of considerable duration, since the stage is found in great abundance, and the oosphere wall develops perceptibly at this time. During this period of quiescence the male nucleus enlarges until it eventually equals the female in size (*figs. 37, 38*) or nearly so. Fusion then occurs, both nuclei being in resting condition. An increase in the number of degenerating nuclei occurs in the oosphere simultaneously with the opening of the antheridial tube. This is quite evidently due to supernumerary antheridial nuclei which are clearly introduced (*fig. 33*). These nuclei, although some of them appear perfectly normal, at length degenerate and eventually dissolve, since only one nucleus is to be found when the fusion is complete. There is no evidence of a general fusion such as is described by Hartog (1891) and Golenkin (1900). This species presents a clear case of the presence of fertilized and unfertilized nuclei in the same cytoplasm, and illustrates the inability of the unfertilized nuclei to survive these conditions.

Before the accumulation of food advances far, the fusion nucleus divides, presenting a nuclear figure which is enormous in comparison with those in the oogonium and oosphere (*fig. 40*). As these divisions succeed one another, the nuclei decrease in size, so that those of the winter spore are about the size of the vegetative nucleus, and are probably about thirty or forty in number (*fig. 41*). Wager (1896) estimated the number in *A. candida* to be thirty-two. In ripening the spore exhibits those changes in wall and contents which characterize the other members of this group.

ALBUGO CANDIDA.

The result of the study of *A. Tragopogonis* suggested that the great variation in mode of fertilization seen in this genus might be explained in a way hitherto unsuspected. I have studied *A. candida*, therefore, comparing it stage for stage with the other species referred to in this paper. My observations essentially agree with those of Wager (1896), which were confirmed and extended by the research of Davis (1900). I have here only to present some further details, to make certain homologies clear, and in no radical way to alter the statements of these two writers.

The initial step in development consists of a differentiation of the ooplasm in the center of the oogonium, the nuclei in the meantime undergoing mitosis. One stage in this process is beautifully figured by Davis (1900, *fig. 2*), and a stage slightly older is herewith presented (*fig. 14*). It should be noted in these figures that the ooplasm is much more vacuolate than in the other known species (*figs. 3, 14, 28*). Particularly in the figure by Davis will it be seen that the ooplasm is separated from the periplasm by a rather broad irregular zone of very dense cytoplasm.

The conditions presented even in this early stage of oogenesis are markedly different from those of the other species. There is apparently no preliminary aggregation of cytoplasm into masses, but rather a simultaneous movement from the oogonial wall toward the center, leaving behind only slender threads of cytoplasm. It appears as though this movement occurs as a wave starting at the oogonial wall and moving so as to crowd the cytoplasm into the dense zone represented in the figures. When this condition obtains, the nuclei are approximately in metaphase, and it is clear that this represents the first nuclear division. Nuclei in metaphase and late anaphase may be seen in the same oogonium, but it is not probable that one nucleus undergoes more divisions than another, since the nuclei simultaneously pass through the stages of early prophase.

At a somewhat later stage, judging by the development of

the coenocentrum, the zone of dense cytoplasm represented in *fig. 14* (Davis 1900, *fig. 2*) disappears. The rudimentary oosphere consists then of uniformly distributed cytoplasm, together with the nuclei which have completed their mitoses (*fig. 15*). This condition is characterized by the well-developed coenocentrum, the presence of nuclei which are not in mitosis, and the central mass of dense, uniform, deeply staining cytoplasm which is suspended from the oogonial wall by delicate threads. Some of the nuclei now enter a second mitosis, and these may be found in various stages lying in this clearly marked central region. Those lying outside in the periplasmic region do not divide again, a distinction which is maintained in all species of Albugo.

Before the inception of this second mitosis, during its progress, or after its completion, the nuclei pass toward the periplasm (*figs. 15–17*) until all but one has left the ooplasm. The plasmoderma[3] is now formed, preceded by the first sharp differentiation of ooplasm from periplasm. This is immediately followed by the wall, a condition illustrated by Davis (1900, *fig. 4b*).

What stage in *A. candida* corresponds to zonation in the other species? Is it the stage represented by *fig. 14*, where the ooplasm is bounded by a dense layer of protoplasm; or later (*fig. 15*) when the oosphere is somewhat more sharply differentiated; or still later when the nuclei have left the central region and the plasmoderma is about to be formed? The stage shown in *fig. 14* has nothing in common with zonation except that the nuclei are in metaphase of the first mitosis. Zonation is chiefly characterized by that sharp differentiation of ooplasm and periplasm which precedes the plasmoderma. This character is absent here, as well as from the stage represented in *fig. 15*. A distinct differentiation does not obtain until all of

[3] The term *plasmoderma* has been suggested to me by Professor Strasburger as a desirable equivalent for the much-abused *Hautschicht*, which was originally intended for purely German usage. From its relation to cell activities (Noll 1888) and its characteristic kinoplasmic content the plasmoderma is to be regarded as a structure quite distinct from that designated by the term *ectoplast*.

the superfluous nuclei have left the ooplasm (Davis 1900, *fig. 3*). This is clearly the stage nearest to zonation in character, therefore, although it differs much from the zonation of the other species in general appearance. The absence of preliminary protoplasmic aggregation precludes the early marshaling of the nuclei into the form of a hollow sphere, a phenomenon which is so characteristic of the zonation stage in *A. Bliti*, *A. Portulacae*, and *A. Tragopogonis*. It may be for this reason, also, that the formation of the plasmoderma is delayed.

The mode of development of the coenocentrum and its relation to the oospheric nuclei remain to be considered. The coenocentrum was first observed by Wager (1896) in *A. candida*, and its development has been more closely followed in the same species by Davis (1900). The structure was given its present name, and its nature and history were discussed to some extent, in my earlier paper on *A. Bliti* (1899). Wager (1900) further notes its presence in *Peronospora parasitica*, and observes that it has there an attraction for the one reentering female nucleus. I have already called attention to the same phenomenon in *A. Tragopogonis*. This attraction is strikingly exhibited in *A. candida*, and demands a somewhat detailed consideration.

A very early stage in development is shown by Davis (1900, *fig. 2*.) In a later stage the coenocentrum contracts, and a large globule appears at its center, much as in *A. Tragopogonis*, with the exception that the coenocentrum is very granular. The granules resemble the nucleoli of this species, both in size and stain reaction. They appear to enter the coenocentrum from the ooplasm in very early stages, and may be seen in great numbers in the adjacent region (*fig. 13*). The nuclei at this period are in mitosis, and it is quite usual to see two, three, or more spindles lying with one apex imbedded in the coenocentrum (*figs. 16, 18–20*). Their form is elongated before their attachment, and it is evident that the coenocentrum possesses an attractive influence. A similar attraction has been observed in *Peronospora parasitica* (Wager 1900) for resting nuclei, and by myself in *A. Tragopogonis;* but the phenomenon

of attraction is exhibited in *A. candida* during mitosis. It often results in a spindle nearly twice the normal length and proportionately narrower. Such cases are represented in *figs. 18–20*. The consequence of mitosis under these conditions is that several daughter nuclei remain anchored to the coenocentrum (*figs. 17, 21, 22*). Whether there is an organic attachment or merely an imbedding of a projection is impossible to say, but certainly these daughter nuclei protrude a long pseudopodium-like extension which penetrates the coenocentrum to a considerable depth. In late stages, as the nuclei pass to the periplasm, fewer are found attached to the coenocentrum, with the result that eventually only one remains. This nucleus enlarges greatly, and is often found lying in the cytoplasm in such a position as to suggest that it had been fixed while swaying to and fro on the stalk-like pseudopodium which attaches it to the coenocentrum. The migration and attachment of the nuclei to the coenocentrum seem inexplicable on any basis save that of chemotactic influence.

The growth of the nucleus while in contact with this structure, both in this species and in *A. Tragopogonis*, gives evidence that the coenocentrum functions as an organ of nutrition for the one surviving nucleus. In some respects the coenocentrum resembles a trophoplast, but the presence of granules, probably of kinoplasmic nature, renders the analogy less complete. It seems also to arise *de novo* in each oogonium, a character not in agreement with the theories most generally accepted. The evidence that such structures always arise from preexisting ones is not conclusive, however, and the work of Davis (1899) on Anthoceros may indicate that the chloroplast in that plant arises *de novo* in each sporophyte from the cytoplasm of the spore mother cells, although the author does not definitely draw that conclusion. If such be the case, the similarity between the coenocentrum and the chloroplast is closer. Evidence of high specialization in chloroplasts is given, moreover, in observations of Oltmanns on Coleochaete (1898), and of Davis on Anthoceros (1899), where the chloroplasts divide in advance of the nuclei, so

as to provide daughter structures equal in number to the nuclei which are to be formed. Considering the coenocentrum as a source of nutrition, the phenomenon of chemotaxis here as affecting the position of the nuclei is quite parallel to that exhibited so abundantly in animal cells, where the nuclei wander toward the source of nutritive supply (Korschelt 1889). The development of the pseudopodium-like structure also has its analogy in the animal cell, where the nucleus becomes amœboid or protrudes many pseudopodia in order to enlarge its absorptive surface (Korschelt 1889). In the nucleus under consideration the nature of the nutriment may render it more advantageous to penetrate by means of one sharp projection. While many plants possess cells having very irregularly shaped nuclei, *e. g.*, endosperm cells of Zea, epidermal cells of Allium, Hyacinthus (Zimmermann 1896), amœboid movements are much more rare in plants than in animals. Kohl (1897) by the action of asparagin has incited such movements in the nuclei of the cells of Elodea and Tradescantia, and considers them comparable with the phenomena observed by Korschelt (1889). This also throws light on the behavior of the nuclei in Albugo. Kohl considers with Korschelt that the amœboid movement stands in direct relation to the heightened exchange between nucleus and cytoplasm.

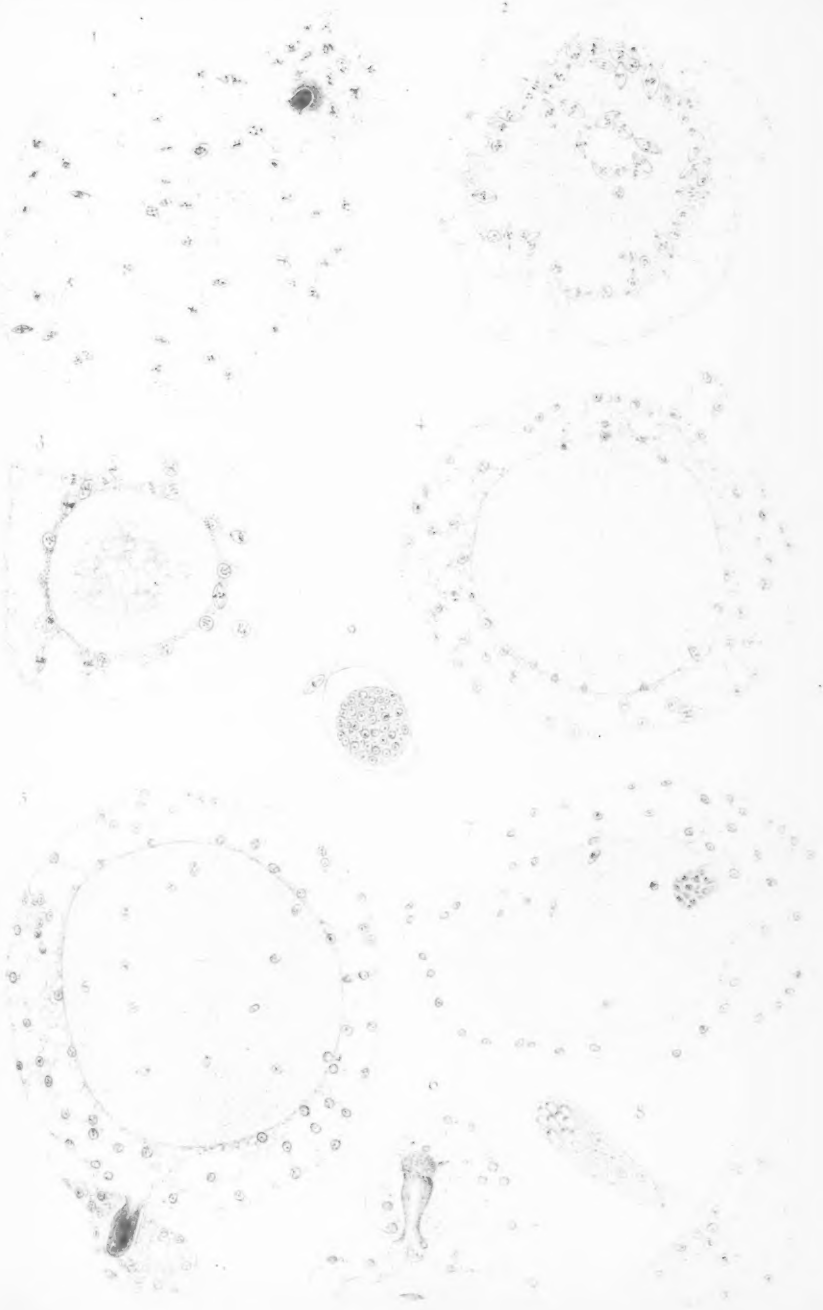
The coenocentrum may in a sense be likened to some of the so-called yolk nuclei, or *Dotterkern* of animal eggs. In *A. Bliti* (Stevens 1899, *fig. 69*) and in *A. candida* (Davis 1900, *fig. 2*) there is slight indication of radiate structure which somewhat resembles the figures of Munson (1898) illustrating the yolk nucleus of Limulus. The structures agree in having nutritive functions. In certain cases, as in Limulus and the newt (Jordon 1893), the yolk nuclei seem to develop directly from the cytoplasm, and in this further resemble the coenocentrum. A comparison of these structures emphasizes the fact that protoplasm in diverse organisms under certain conditions may become similarly differentiated for the performance of particular functions.

Concerning the antheridial tube there is but little to add.

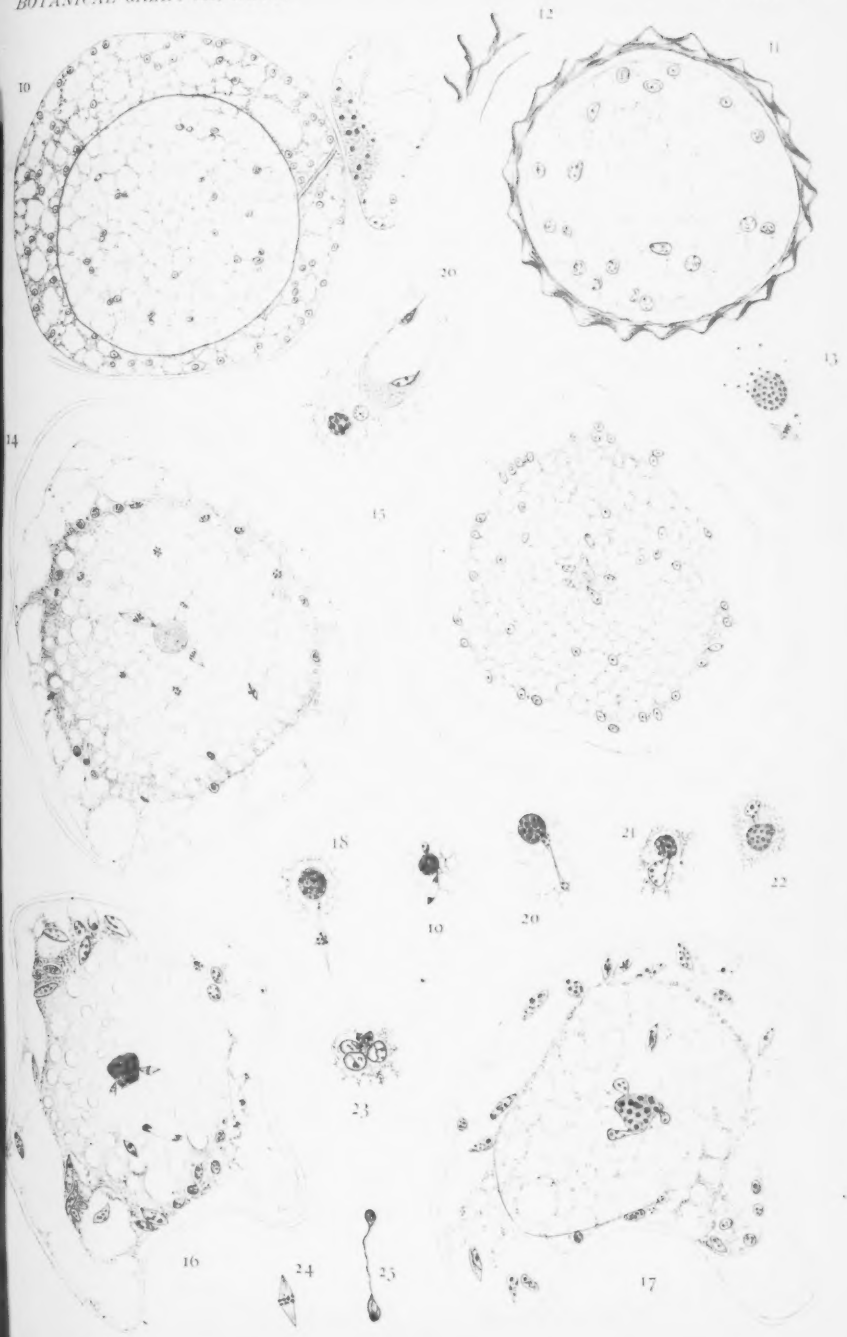
Both Wager (1896) and Davis (1900) assert that it bears one functional nucleus, but they figure other nuclei in the neck of the tube, and Davis suggests that occasionally more than one nucleus from the antheridium may enter the ooplasm. *Fig. 26* shows a case where the tube clearly contains one large male nucleus in a mass of dense cytoplasm, and another nucleus lying in such a position that it must be set free were the tube to open. It is also common to find more than two nuclei in the oosphere just after the opening of the tube and before fusion. In such cases it is evident that there is a supernumerary nucleus, but whether it is derived from the antheridium or the oosphere is not always plain. Such conditions as those shown in *fig. 17* render it probable that sometimes two or even more female nuclei might survive. The supernumerary nuclei would then be found near the coenocentrum (*fig. 23*). Occasionally the one supernumerary nucleus lies free in the ooplasm at a considerable distance from the coenocentrum, and is probably of antheridial origin. It is quite conceivable, and it may occasionally happen, that two functional nuclei are derived from each organ, and that a multiple fusion of nuclei may occur even in *A. candida*.

Figs. 24 and *25* represent two stages in the division of the fusion nucleus. The strongly thickened fibers and their contorted condition agree well with the view of Drüner (1895) that the spindle poles are separated by a push due to an elongation of the spindle, not by a pull from a region external to the nucleus, nor by cytoplasmic streaming. The division is of quite the same type as that exhibited before fusion, an agreement that is particularly evident in anaphase, so characteristic in both this and other species.

A fuller study of the species has developed one essential point somewhat at variance with previous observations. I believe I have shown that there is no time when the central region in *A. candida* is entirely devoid of nuclei, and that very early there is an attractive force exhibited by the coenocentrum which results in a retention of one nucleus while the others are



ALBUGO PORTULACAE.



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ALBUGO CANDIDA.

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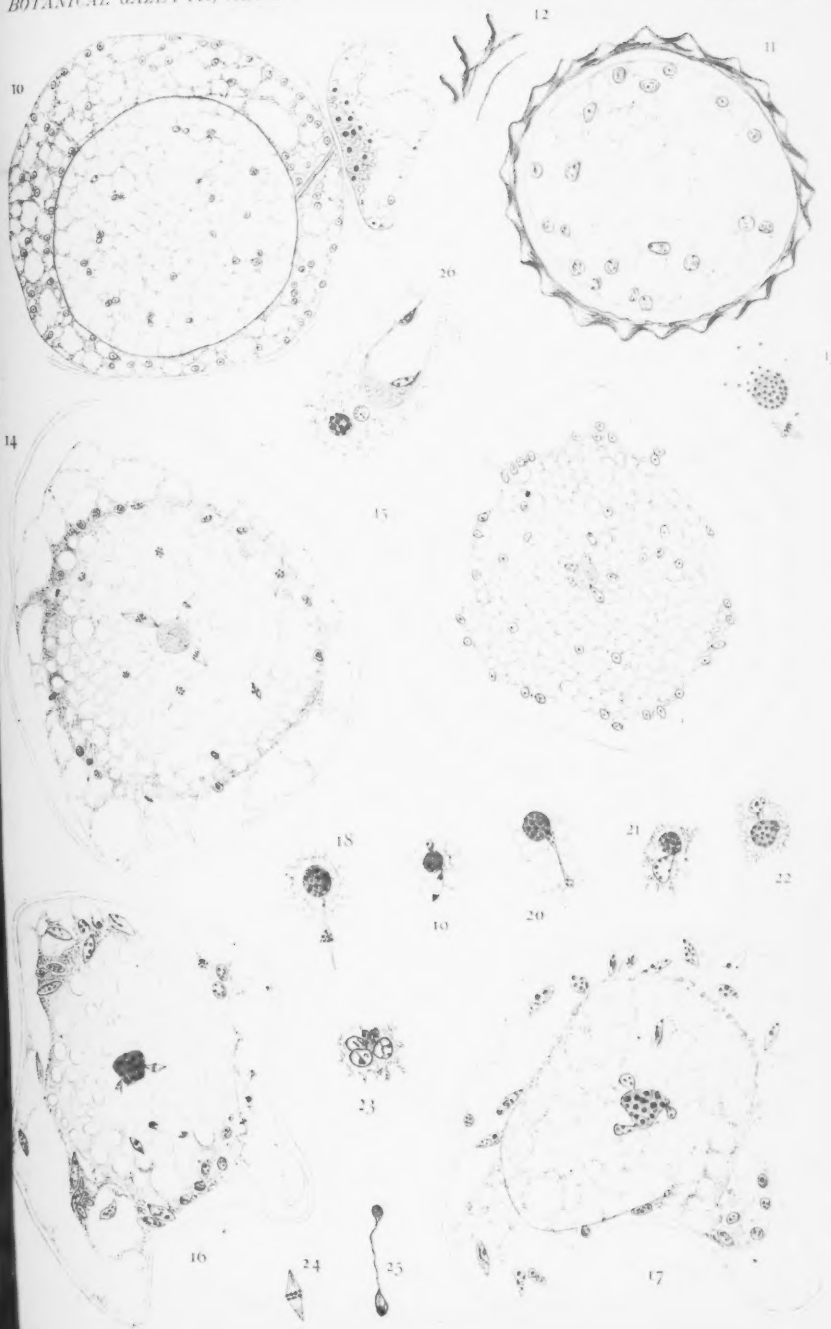
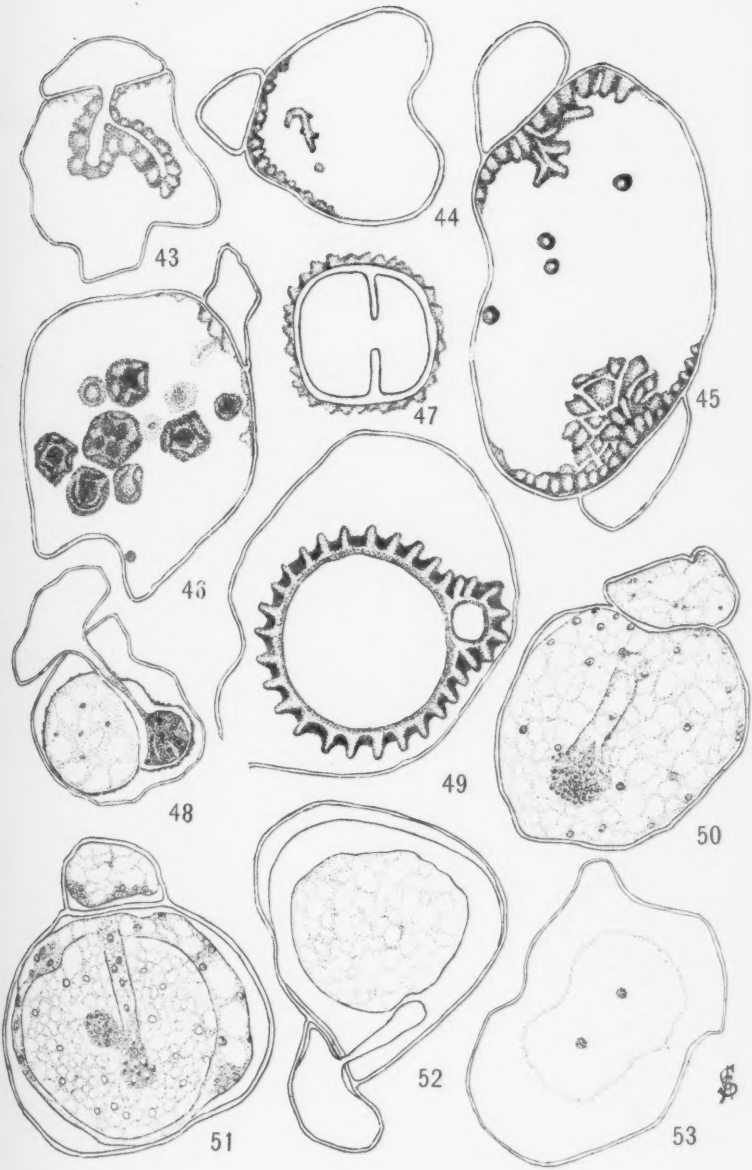


FLS

ALBUGO CANDIDA

FIG.

ALBUGO TRAGOPOGONIS.



STEVENS on ALBUGO

carried outside of the region of the oosphere. In this respect *A. candida* differs from the other species of Albugo.

SUMMARY.

Albugo Portulacae.

1. *A. Portulacae* possesses a multinucleate oosphere which develops in a manner very similar to that of *A. Bliti* (Stevens 1899), *i. e.*, the nuclei all pass to the periplasm, dividing mitotically; and some of the daughter nuclei reenter the ooplasm, divide again, their products becoming the female nuclei, the plasmoderma being differentiated in the meantime.

2. Two mitoses occur in both oogenesis and spermatogenesis.

3. The nuclei return to the ooplasm after division much diminished in achromatic content.

4. The nuclear figure of the second mitosis is clearly distinguishable from the first by the diminished kinoplasm.

5. The antheridial tube is multinucleate.

6. The numerous antheridial nuclei fuse in pairs with the numerous oospheric nuclei, the number of fusion nuclei being usually larger than in *A. Bliti*. These fusion nuclei pass the winter without further change.

7. A coenocentrum somewhat less highly developed than that of *A. Bliti* is present.

8. The receptive papilla in *A. Portulacae* is larger than in the other known species.

Albugo Tragopogonis.

9. A multinucleate oosphere develops in the same manner as in *A. Bliti* and *A. Portulacae*, and is then reduced to a uninucleate condition by disorganization of the supernumerary nuclei.

10. The nuclei pass to the periplasm, divide, and return to the ooplasm much diminished in achromatic content.

11. Two mitoses occur in oogenesis and spermatogenesis.

12. The nuclear figure of the second division may be distinguished from the first by a diminution of kinoplasm.

13. The antheridial tube conveys one or more nuclei into the oosphere where one fuses with the female nucleus.

14. Supernumerary male nuclei disorganize as do the supernumerary female nuclei.

15. The fusion nucleus undergoes repeated mitoses, and the winter oospore is consequently multinucleate.

16. The coenocentrum is very highly developed. It possesses an attraction for the primary oospheric nuclei and serves as a source of nourishment for the surviving female nucleus.

Albugo candida.

17. The oosphere is developed in a manner quite different from that seen in *A. Bliti*, *A. Portulacae*, and *A. Tragopogonis*. The periplasm and ooplasm are not differentiated until the second mitosis is completed. The nuclei, excepting one, eventually pass to the periplasm, which is then cut off by a wall.

18. One nucleus remains in the oosphere attached to the coenocentrum.

19. The coenocentrum attracts the nuclei very strongly, and later serves as a source of nourishment for the surviving female nucleus.

20. The antheridial tube occasionally contains two nuclei.

[*To be continued.*]

BOTANICAL INSTITUTE, BONN.

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX.

WILLIAM L. BRAY.

(WITH TWENTY-FOUR TEXT FIGURES)

WESTERN Texas has been a choice field for botanists from the earliest days, always having been accessible through the numerous army posts and government surveys. For this reason the flora early became fairly well known through numerous contributions describing the country and its vegetation, and from descriptions of species, culminating in the *Botany of Western Texas* by Professor Coulter. Since that time, the study of plants in their natural environments has enriched botanical thought, and it seems opportune to take up again the flora of western Texas and to apply to it the new methods.

A further reason for presenting the plant life of Texas as the product of its environment lies in the growing tendency to rely upon such study to furnish a rational basis for the exploitation of plant life in agriculture, horticulture, forestry, agrostology, and various other economic fields. The great diversities of climatic factors, of soils, and of physiographic conditions in the Texas region make it necessary to find the results of these factors as recorded in plants already occupying the field, that they may serve as a guide in attempting to introduce new ones. The statement that the flora of western Texas early came to be fairly well known is true only of pteridophytes and spermatophytes, for the bryophytes and thallophytes have scarcely been noticed thus far.

The present paper aims only to clear the field a little, preparatory to its cultivation along special lines; and because it is a very large field, with much to be done, it offers a strong

invitation to colaborers. There is no special reason for excluding eastern Texas from this discussion, other than that the whole field is too large for a single paper. During a residence of more than three years, the writer has personally explored a great deal of the state, and yet there are vast areas he has not seen, and of which he cannot speak from first-hand knowledge. Hence even this general analysis of the vegetation must contain inaccuracies and misjudgments, which only a detailed survey of the provinces concerned will correct.

With the opportune appearance of Professor Hill's *Physical geography of the Texas region*[1] the task of presenting the climatic and especially the physiographic and geological factors has been much lightened, and by his courtesy a very free use has been made of this Texas folio. He has given much help also in the way of suggestions and photographs, which is herewith gratefully acknowledged. Dr. V. Havard's *Report of the botany of southern and western Texas*[2] has also been of great service.

The order followed is to discuss first the climatic factors in their relation to the vegetation of the region, and second the vegetation itself under several general types of association (plant formations), together with the factors of geology, soils, and physiography (edaphic factors), which determine chiefly the type of formation upon any given area. Omitting from consideration practically all of the Texas region lying to the east of meridian 97°30′, we have to deal with an area covering in its greatest north-south dimensions 10.5° of latitude (from about 26° to 36.5°), a fact of no small significance in climatic zones; and in its east-west extent 9° (from 97.5° to 106.5°), a distance sufficient to carry the western border into the Pacific zone.

CLIMATIC AND EDAPHIC FACTORS.

TEMPERATURE.

In the facts that the southernmost point of Texas is at sea level and borders on the Gulf, and is but 26° north of the equator;

[1] U. S. Geological Survey. Texas folio. 1900.

[2] Proc. U. S. Nat. Mus. 8:—. 1885.

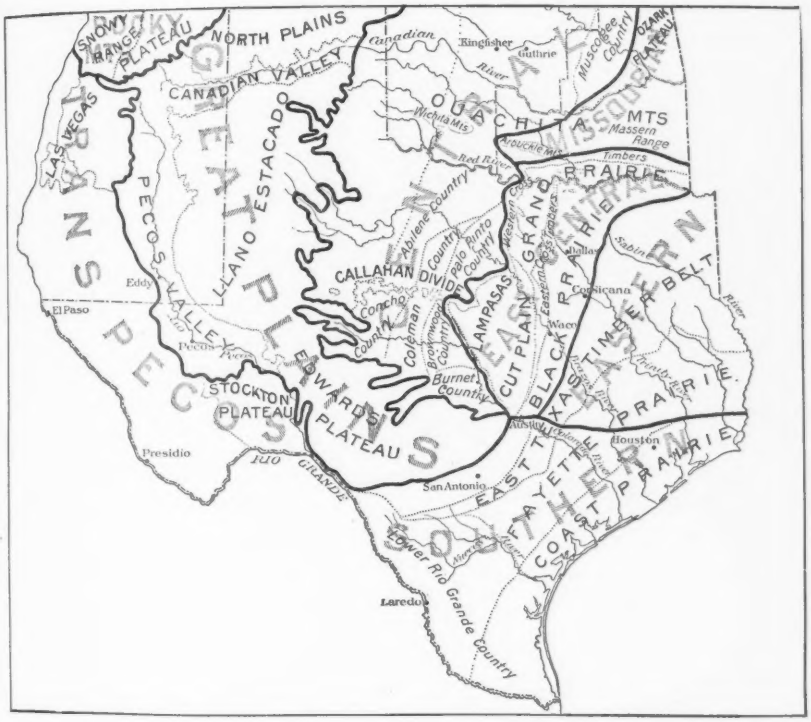


FIG. 1.—Physiographic provinces and minor subdivisions of the greater Texas region.—From Hill's Phys. Geog. Texas.

that the northernmost part is 10.5° removed from this, is at an elevation of 5000 feet, and directly exposed to the extremes of continental climate; and that in the latitude of 32° a mountain mass reaches the height of 9000 feet; we have an indication of the range of annual temperature for the region under discussion. The temperature conditions of the lower Rio Grande valley from October to April are about the same as those of the middle third of the Florida peninsula. Those of the Staked plains above 4000 feet are about the same as those of the southern half of Kansas, Missouri, and Illinois. Again, the daily

extremes, which are reflected in the structure of species, stand out most significantly in a comparison of two extreme points. The greatest daily fluctuation at Galveston is 5 to 7°F. in April; at El Paso 25 to 27° in June–July. During the February norther of 1899, points on the Staked plains above 4000 feet registered more than 20° below zero, and it was 12° above at Brownsville on the same date. These figures indicate the extremes which may occur to bring about a periodic reduction of the Austral flora. The following temperature zones as measured by the flora prevail in the western Texas region.

DILUTE XEROPHYTIC TROPICAL.—This can be recognized only in the extreme southern part of the Rio Grande embayment, especially in the present Rio Grande valley. The mean annual temperature of the valley, however, from Laredo to the mouth, is 73°, slightly below that of southern Florida. The monthly means correspond to those of the middle part of the Florida peninsula from September to March, except the January mean which falls some degrees below. The summer means rise much higher than in any part of Florida. A record of sixteen years at Brownsville showed a minimum temperature of 18° (the minimum in February 1899 was 12°) and five years without frost. At Indianola a record of fifteen years showed a minimum of 15° and four years without frost. Probably a freeze severe enough to kill tropical woody vegetation occurs in periods of ten to twelve years. The fatal temperature for tropical plants in this region is that due to the northers, which bring abnormally low temperatures suddenly, and not infrequently during the growth season. The actual poverty of a tropical flora, however, is due equally to the aridity of the region. The floral affinities of the tropical element are with the Neotropical Gulf zone, and are a part of the Tamulipan division of this zone.[3]

The following species, as illustrations, will be recognized as belonging to groups of chiefly tropical distribution, but even some of these pass into northern and southern subtropical territory: *Sabal Adansonii*, *S. Mexicana*, *Monanthochloa littoralis*,

[3] MERRIAM, C. H.: Life zones and crop zones, p. 52.

Jatropha macrorhiza, *J. multifida*, *Janusia gracilis*, *Aspicarpa hyssopifolia*, *A. longipes*, *Galphimia angustifolia*, *Malpighia glabra*, *Amyris parvifolia*, *Helietta parvifolia*, *Schaefferia cuneifolia*, *Serjania incisa*, *S. brachycarpa*, *Urvillaea Mexicana*, *Wissadula mucronulata*, *Hermannia Texana*, *Melochia tomentosa*.

SEMITROPICAL.— The tropical elements, which are but faintly indicated even in the southernmost part of Texas, quickly merge into a semitropical zone, which is visible and persistent even to the cañons on the border of the plains region, and especially up the Rio Grande into the Great Bend and its side cañons, and in the lower Pecos cañon, and this in spite of the great preponderance of Sonoran species of the Lower Austral. The range of *Acacia Farnesiana* and *Parkinsonia aculeata* would represent fairly the area of this zone outside the Rio Grande valley. A number of the species included in genera cited for the tropical portion extend also over this area. It is further indicated by such genera as Guajacum, Mortonia, Pistacia, Peganum, Ascyrium, Persea, Myrica, Balodendron (listed by V. Bailey from Corpus Christi), Cardiospermum, Castela, Choisya, Hermannia, Ayenia, Corchorus, and Malachra.

LOWER SONORAN.—The Lower Sonoran elements so pervade the regions containing tropical and subtropical species as to be by far the dominant flora, and to constitute the characteristic formations. If the Lower Sonoran division of the Lower Austral zone be counted from the 98th meridian in Texas, it exists in several grades of purity or intensity over the following provinces, varying with differences in temperature, moisture, and soil: (1) the Rio Grande plain, especially interior to the tropical and subtropical divisions; (2) the erosion mountainous portion of the Edwards plateau; (3) the central plains of northern Texas (including the cañon of the Canadian river across the Staked plains); (4) the Staked plains below 3500 feet and the adjoining plateau prairie to the south; (5) the Toyah basin; (6) the bolson plains and mesas of trans-Pecos Texas; (7) the Stockton plateau and slopes of the Guadalupe, Davis, and other mountains at the north up to about 4000 feet, and the slopes of

the Chisos and other mountains in the Great Bend up to 6000 feet.

Of these several provinces, each of which possesses distinctive floral or physiological conditions, the Rio Grande plain is clearly related to the tropical and the subtropical in its prepon-

FIG. 2.— Geology of the greater Texas region; *1*, Older Granites; *2*, Palaeozoic and Mesozoic; *3*, Cambrian and Silurian; *4*, Carboniferous; *5*, Permian; *6*, Jurassic; *7*, Lower Cretaceous; *8*, Upper Cretaceous; *9*, Non-marine Tertiary; *10*, Marine Eocene; *11*, Coast Neocene; *12*, Later igneous.— From Hill's Phys. Geog. Texas.

derance of Mimoseae and Caesalpineae, of Rhamneae, Zygophyllaceae, Rutaceae, Simarubaceae, Malvaceae, Euphorbiaceae, Nyctaginaceae, and similar groups. The central plains of the north, on the contrary, possess a minimum of these groups, but more which are peculiar or common to the central prairie plains of Kansas, Missouri, Indian Territory, and Oklahoma, such as Compositae (certain subfamilies), Papilionaceae, Onagraceae, and others. The identity of plant formations, however, as

exhibited in their general aspect, is the most convincing demonstration of the identity of this region with the northern prairies, and its small affinity with the southern ones. The cultural possibilities still further emphasize the extremes of these two divisions of the Lower Sonoran zone. As regards moisture conditions, both are transitional between Austro-riparian and Lower Sonoran, but the Rio Grande plain is in the zone of rice, cotton, sugar cane, of fruits like the fig and pomegranate; while the northern prairie province is in the belt of corn, wheat, and oats, and of such fruits as the apple. In short, the two provinces are transitional both as to temperature and moisture zones, the Rio Grande to the semi-arid and arid tropical, the central prairies to the Upper Sonoran and Carolinian zones.

The extreme in the direction of Lower Sonoran arid conditions is reached in the bolson desert provinces of trans-Pecos Texas. Certainly westward of the prairie plains of the Stockton plateau one is within the arid plateau province of that part of the Lower Sonoran zone, which then prevails westward to the Pacific. Indices of this arid province are the Yucceae, Agaveae, Cactaceae, and genera like Fouquiera, Larrea, and Flourensia. Elements of this extremely arid portion overlap to some extent portions of the Edwards plateau and of the south debris slope of the Staked plains, as will be seen subsequently. Finally, the entire area covered by the Lower Sonoran provinces is occupied by the single and generally dominant *Prosopis juliflora* (mesquite), which, though dependent upon certain peculiarities of soil structure, is absent from no considerable portion of the zone, and in its growth and occurrence reflects the measure of climatic conditions prevailing in the several provinces. This species marks well the transition from Lower to Upper Sonoran on the Staked plains.

Upper Sonoran.—This zone occupies the Staked plains and Panhandle above 3500 feet, the higher slopes and summits of the Guadalupe (except the highest points in the range), Davis, and other northern mountains above 4000 or 4500 feet, and of the Chisos mountains in the Great Bend above 6000 or 7000

feet. The summit of the Staked plains above 4000 feet has, as regards temperature, the climate of the southern half of Kansas, Illinois, and Missouri; but on account of low average rainfall and prevailing high southwest winds it has the characteristics of the high plains climate of western Kansas and Nebraska. In trans-Pecos Texas the Upper Sonoran zone is a series of islands represented by the isolated mountain summits rising out of the Lower Sonoran zone.

TRANSITION ZONE.—The highest peaks of the Guadalupe and Davis mountains possess a considerable number of transition herbaceous and shrubby species ranging north in the mountains of Montana and Washington, beside forest tracts of *Pinus ponderosa*, *P. flexilis*, and *Pseudotsuga taxifolia*, which are typical transition forests.

FLUCTUATIONS IN ZONAL BOUNDARIES.—If we accept the law of temperature control "that the distribution of boreal species southward is limited by the mean temperature of a few weeks during the hottest part of the summer," those annuals which begin their activity at a relatively low temperature, and complete their vegetative and fruiting period before the approach of summer temperature, would enjoy a distribution far within the Austral regions. To state the case differently, within the Lower Sonoran or semi-tropical zone the lower temperature prevailing during February, March, and April, in which certain boreal species complete their period of fruition, would be for such species as truly a boreal zone as if they completed their fruition period during April, May, and June in correspondingly higher latitudes. This fact can account for the presence of such species as *Evax prolifera*, *Draba cuneifolia*, *Anemone Caroliniana*, *Corydalis aurea*, *Linaria Canadensis*, and others, within the borders of the semi-tropical zone. These all come into flower in the last half of February. This also explains how many prairie annuals, which are so abundant in their season as to give the dominant tone to the vegetation, may appear in this way successively over the whole Great plains area and south to Brownsville, or more frequently over the central prairies of Kansas, Missouri, and

Indian Territory to the southern extremity of the Rio Grande plain.

MOISTURE, WIND, AND LIGHT.

MOISTURE.

RAINFALL.— Beginning with an average fall of about thirty inches at the 98th meridian, the annual rainfall of the west

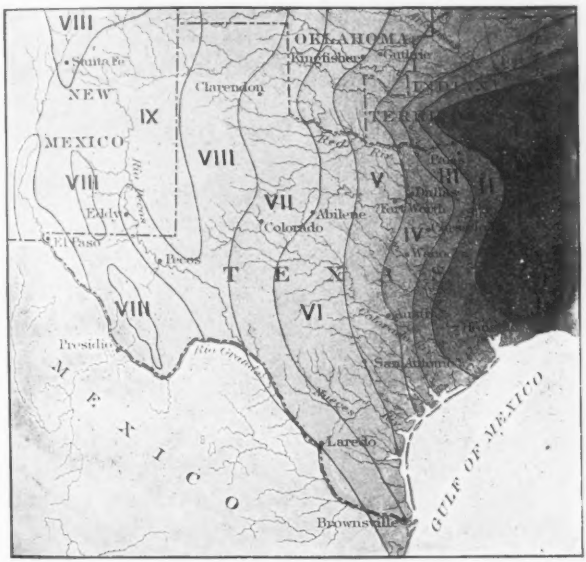


FIG. 3.— Precipitation in the Texas region: *I*, over 50 in.; *II*, over 45 in.; *III*, over 40 in.; *IV*, over 35 in.; *V*, over 30 in.; *VI*, over 25 in.; *VII*, over 20 in.; *VIII*, over 15 in.; *IX*, over 10 in.— From Hill's Phys. Geog. Texas.

Texas region decreases to nine inches at El Paso. This decrease is in general so uniform that the state may be divided into north and south zones of precipitation of five inches difference in the annual amount. The organization of vegetation with respect to moisture emphasizes these zones. The greatest interruption in their north-south equality occurs in the Guadalupe and Davis mountains, where the rainfall on the summits is fully double that of the bolson plains between the ranges (*fig. 3*).

Of equal importance with the total quantity of rainfall for plant life is its seasonal distribution. Even in the eastern part of the area this is irregular and spasmodic, although a sufficient quantity falls on the average to maintain a fairly large percentage of mesophytic species of the Mississippi valley and Gulf regions (Carolinian and Austroriparian zones), and to insure reasonable certainty of yield from cotton, corn, wheat, and oat crops. But the vegetation west of the 98th meridian bears the marked individuality of the Lower Sonoran zone in its physiological adjustment to arid conditions.

Texas lies in a peculiar position with regard to atmospheric movements, which may account for the periodic and excessive variations in seasonal and annual rainfall. The El Paso region is clearly within the Pacific-Lower Californian field of climatic influence, while the Rio Grande plains province is mostly in the Mexican climatic zone. The Great plains type of rainfall predominates over the Staked plains, and generally far into the center of the state. The Gulf type scarcely extends west of the Balcones escarpment and Grand prairie, but occasionally it carries a season of high rainfall well toward the central provinces, as during the season of 1900 (*fig. 4*).

The mean annual rainfall at Austin is 38.88 inches. Its lowest record is 18.33 inches in 1879, and its former highest record, 51.79 inches in 1888, was exceeded during 1900. The rainfall from January 1 to November 1, 1900, reached 51.19 inches. This is a fluctuation equal to the total mean. The fluctuation between Gulf and Mexican type is shown in a remarkable degree at Brownsville, where the mean is 31.52 inches, the minimum 8.88 inches in 1870, and the maximum 60.06 inches in 1886, a variation of 167 per cent. of the mean. The amount of rainfall in a single month and its departure from the monthly average may be excessive. In the last case cited (Brownsville), the rainfall for September 1886 was 30.57 inches, or 23.27 inches above the September mean. The June rainfall at Fort Clark in 1899 was 22.32 inches, or 19 inches above the mean, over 75 per cent. of this excess falling in twenty-four hours. It thus appears that

not only are the fluctuations extreme, but that a large percentage of the season's rainfall may be precipitated in two or three heavy thunderstorms. The effect of the consequent erosion is of significance for vegetation under certain soil conditions, as for example in the Red beds province, and in other places where too heavy pasturing has bared the ground of the soil-

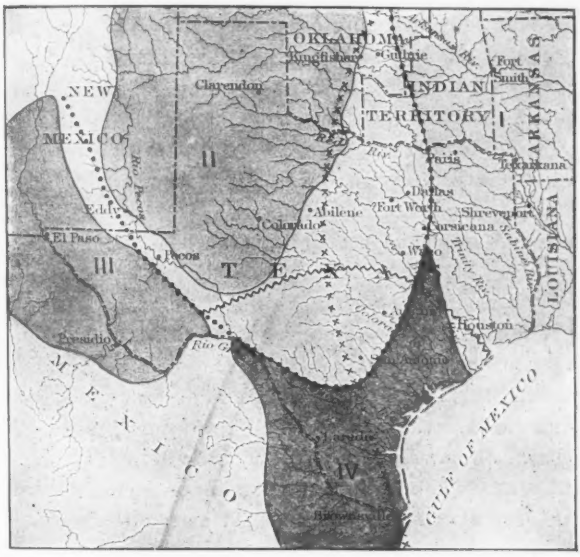


FIG. 4.— Types of rainfall in the Texas region: *I*, Gulf; *II*, Great Plains; *III*, Yuma; *IV*, Mexican; ×××, western margin of Gulf; ..... southern margin of great plains; ~~~~~, northern margin of Mexican.— From Hill's Phys. Geog. Texas.

building grasses, as in the upper Rio Grande province. From these irregularities it follows that the vegetation has adapted itself to continuous drouths, and to sudden transitions from growing to dormant periods and back again.

SOIL MOISTURE.— The relation of rainfall to vegetation after its precipitation is of importance, and is largely a result of geological structure and relief. A single illustration will suffice. In traversing the Rio Grande plain from Uvalde to Eagle pass

in April of the dry spring of 1898, all the country covered by compact clay silt wash from the Balcones escarpment, being soil from which rainfall quickly flows away, was practically bare of grass and herbaceous vegetation. Even the streamway timber vegetation was shedding its leaves. On the outcrop ridges of Eocene sand, where all precipitated moisture had been retained and kept available, the landscape was fresh with grasses, composites, legumes, and many other annuals. This was repeated in a more noticeable degree during the same month in passing from Eagle pass to Carrizo springs, where again the compact clay and silt alternated with wide stretches of Eocene sand. The availability of underground water in the sand beds is evidenced by innumerable wind pumps, while in the clay silt country the surface water is collected in ponds.

HUMIDITY AND EVAPORATION CAPACITY.— The conditions of air moisture in the west Texas region have an important bearing upon the vegetation. As may be noted in *fig. 5*, illustrating evaporation capacity, this increases in proportion to the decrease in rainfall, reaching its maximum of 80 inches at El Paso, with this important exception, that in the high mountains of the Guadalupe and Davis ranges, where the rainfall is double that at El Paso, the evaporation capacity is 90 inches annually. This moistureless condition of the air under these circumstances reacts in several ways to pile up extremes of aridity. First, there is no blanket of vapor or clouds, so that the force of the sunlight is intense: and second, temperatures become extremely high during the day, and because of rapid radiation sink to a low point at night, except in the region of the Gulf winds. Under such circumstances the adaptations in the structures of plants are most strongly marked. It follows that moisture determines, far more than any or all other factors, the structural aspects of the flora.

Moisture determines, as we have already seen, degrees of intensity of the Lower Sonoran flora. Lack of moisture has diluted the tropical elements, the Gulf zone semitropical, the Austroriparian and Carolinian floras in the east, and the mountain

transition flora in the west, all of which gradually disappear in the prevalence of intensely xerophytic species. On the other hand, increasing aridity has intensified the Mexican semitropical, the south plateau Sonoran flora, and the Great plains flora. The transition from the eastern mesophytic to the western xerophytic zones presents interesting phenomena of geographic range. For

FIG. 5.—Evaporation in the Texas region, in inches per year.—From Hill's Phys. Geog. Texas.

example, *Juglans nigra* is succeeded by *J. rupestris*, and *Juniperus Virginiana* by *J. sabinoides* and other species. Prominent Austro-riparian and semitropical species, like *Pinus palustris*, *Magnolia grandiflora*, and *Persea Borbonia*, abruptly stop; and xerophytic Lower Sonoran and semitropical species as abruptly begin, as *Prosopis juliflora*, *Acacia Farnesiana*, and *Parkinsonia aculeata*.

WIND.

The enormous expanse of the plains area in Texas and the daily heating of a thinly covered soil promote movements of

air of very effective velocity, especially during the most active growing season. The average velocity per hour for the Gulf coast at Port Lavaca (observations taken formerly at Indianola) from January to July is fourteen miles, at Fort Elliott in the Panhandle 13.4 miles, at Abilene in the central plains province 11.9 miles. The prevailing direction in these cases, and for all the area east of the Staked plains and the Pecos river, is from the southeast, except for Fort Elliott, where the winds during January, February, and March are from the northwest (of little significance as they precede the season of growth). On the summit of the plains the velocity is even higher, and the prevailing direction during the growth period is from the southwest and west. The winds of trans-Pecos Texas are also prevailingly southwest, so that for the Staked plains and trans-Pecos Texas the winds are relieved of their moisture by long passage over arid plateau country. East of the Staked plains and of the Pecos the prevailing wind is from the Gulf.

The significance of these winds for plant life is as follows: (1) in their mechanical impact upon plants; (2) in rapidly carrying away moisture; (3) in erosion and transportation of soils; (4) in moisture-bearing capacity. As to the first point, the result is to dwarf and minimize arborescent growth, and to exclude plants with broad foliage, or herbaceous plants of tall growth. Trees on the coast prairie always incline strongly to the northwest, as does also the prairie mesquite in the Abilene country. On the summit of the plains, even with irrigation, groves of trees are very difficult to start because of the whipping, and bruising, and breaking of young branches and foliage by the wind. On the coast prairie windbreaks are essential in cultivating orchards. At Alvin the orchards where unprotected by windbreaks dwindle away toward the southeast exposure.

As the final effect of high wind is to promote rapid transpiration, this danger results in plants with sparse foliage of small sized leaves. This is brought about also by prevalent or frequent extremes of aridity due to intense heat and lack of precipitation throughout the region of high wind velocity.

In the third place, the transporting power of the wind has a marked influence on the selection of species. First, by dune formation and the assemblage of characteristic dune species, but particularly of sand-binding plants. This is true on the Gulf and on sandy stretches in the interior (Staked plains sand area, Rio Grande sand areas). In the second place, by the erosion and blowing away of soil-forming débris which tends to accumulate upon and modify arid patches, thus rendering the substratum almost naked rock or chalk or gravel, and inducing a new vegetation. The process of wind denudation is much more common, since after over-pasturing and dry weather thousands of acres are left unprotected by soil-binding grasses, and the soil being often a loose, fine silt, or adobe of sandy nature, is easily lifted by even a moderate breeze. It was shown above that such soils are also greatly washed by the heavy rainstorms which come at irregular periods.

As to the moisture-carrying capacity of the winds, of course the Gulf wind starts inland fairly well saturated, but meeting constantly warmer and drier conditions its relative humidity is greatly decreased, so that a precipitation of the moisture of a direct Gulf wind is not common.

LIGHT.

It would be of value if there were definite quantitative data as to the effect of light upon the vegetation of western Texas. Undoubtedly its effect is felt in the general dwarfing of the vegetation, and is plainly seen in the peculiar types of arboreal vegetation, as the "orchard tree" outline of crown. This is observed characteristically in the mesquite, but the live oak, water elm, post oak, and hackberry also assume this form. The mountain cedar is a compact low tree of oval or spherical outline, with diffuse branching from the ground. Undoubtedly the dull grayish-green of the vegetation is largely due to the effect of light, as there are probably fewer chloroplasts in any given assimilative cell. Also there are cases where the epidermis is so constituted as to diffuse light rays by reflecting facets, as appears to be the case in many cactuses and agaves.

A series of experiments was conducted by Professor H. Ness[4] to determine certain differences between the growths from seed of the same varieties of corn grown at Ithaca, New York, and at College station, Texas. Among other things, he showed conclusively that in Texas all varieties have a much shorter stalk than in New York, which he concluded was due to differences in the relative intensity of light, thus verifying previous observations.

In the trans-Pecos country the percentage of sunshiny days is nearly as great as in the maximum region of central and southern California. Where the Gulf winds prevail, there is a relatively high percentage of cloudiness and humidity, which reduces the total light effect. But the percentage of sunshiny days does not express the real effect of light upon vegetation in this region; it is the actual intensity or quantity present at any given hour of sunshine. The sun's rays are almost at the maximum intensity during the vegetative season, and their intensity is undiminished by atmospheric moisture over most of the area. Furthermore, the rock, gravel, chalk, or clay, lacking a green covering of vegetation to receive and subdue the light, reflect it in blinding intensity. Partly on this account, and partly because of lack of air, moisture, and rainfall, there is no densely shading vegetation characteristic of the region except in well-watered cañons. The dominant mesquite, huisache, retama, and numerous other Mimoseae, with their feathery foliage only loosely filter the light, but do not interrupt it. The junipers and pines of the hills and mountain slopes of the Lower Sonoran zone are also relatively shadeless trees, and the scrub oak and the chaparral species generally cast only a thin shade. As a consequence, the shade loving plants west of the 98th meridian are confined to moist crevices or watered cañons and sheltered water courses. This feature is emphasized by the absence of shade loving pteridophytes, and the general occurrence on the exposed rock of eroded areas of sun loving ferns and club mosses.

[4] Transactions Tex. Acad. Sci. **2**: [part 1]. 1898.

PHYSIOGRAPHY AND GEOLOGY.

In general the "greater Texas region" of Hill, to borrow his illustration, lies as a stairway leading from the coast by a succession of steps to the cordilleras. On the west there is a balustrade formed by the southern prolongation of the Rocky mountain cordilleras and plateau; on the north the balustrade is the Ouachita system, extending east and west in Oklahoma and the Indian Territory. The slope leads up from the Gulf level to 5000 feet at the base of the cordilleras at the northwest. The geological areas are the "stair steps," speaking approximately. Beginning with the latest, they are the coastal plain (coast Neocene), the Fayette prairies (marine Eocene), the Black prairie (Upper Cretaceous), the Grand prairie (Lower Cretaceous), the denuded areas of the Granite country, the Carboniferous sandstones and shales, the Red beds (Permian), and finally the Llano Estacado (non-marine Tertiary). The "balustrade" of the trans-Pecos mountains and plateaus (except the Stockton plateau, which is part of the Great plains area) is quite distinct from the regions just cited. The tilting of the strata and weathering and erosion have given rise to diverse physiographic features, which are in close harmony with the geologic structures and strongly reflected in the vegetation (*figs. 1, 2*). Since the edaphic factors stand out so prominently in determining plant formations, they will be given a proportionate prominence in this discussion. In general, the physiographic and geologic provinces as defined in Hill's *Physical geography of the Texas region*[5] are employed in this paper, except that the Great plains region is made to include all east of the front ranges of the trans-Pecos Texas and north of the Rio Grande plain, with meridian 97.5° as an arbitrary boundary on the east. This is done because the physiographic ecology of the vegetation is most significant when it is borne in mind that the present conditions are but a stage in the leveling down of a former higher plain which covered this entire area, and whose remnants we have in the Great plains proper, the Edwards plateau, and buttes

[5] Topographic atlas of the U. S. Texas folio.

and mesas scattered all over the central prairie provinces. The process of leveling is in various stages in different places, such as deep dissections in the southern half of the Edwards plateau, undulating prairie in the Grand prairie province, a flat plain in the granite area with rugose surface caused by projecting granite

FIG. 6.— Vegetation provinces of the west Texas region, chiefly on the basis of physiography and geology: *1* to *1b*, Rio Grande plain, chaparral region (*1*, Lower Sonoran transition to Austro-riprarian and semi-tropical; *1a*, semi-tropical, *1b*, dilute xerophytic tropical); *2* to *2i*, Great Plains region (*2*, Edwards plateau xerophytic timber province; *2a* Edwards plateau plains, grass formations; *2b* Grand prairie transition, between Lower Sonoran and Austro-riparian, grass formations, adobe vegetation, butte and escarpment timber; *2c*, post oak formation on granite, Carboniferous, and upper cross timber sands and gravel; *2d*, grass prairie formations of Red beds province, Lower Sonoran with elements of Upper Sonoran; *2e*, erosion remnants (buttes) of Staked plains and Cretaceous area, xerophytic timber; *2f*, Staked plains Lower Sonoran; *2g*, Staked plains Upper Sonoran; *2h*, Toyah basin, Pecos valley province; *2i*, Stockton plateau province, grass formation and Yucca belts); *3* to *3b*, provinces of Rocky mountains and south plateau slope (*3*, extreme Lower Sonoran, bolson flora, chaparral, Yucca-Agave-Cactus formations; *3a*, Upper Sonoran; *3b*, Rocky mountain transition).

masses. These various phases in the process of wearing away the former plain and leveling up the denuded areas constitute the edaphic conditions which determine the general types of vegetation formation prevailing in the several provinces. These might serve almost equally well as designations of vegetation provinces. The provinces here referred to are the following: the Rio Grande plain; the Great plains region, embracing the Edwards plateau, the Grand prairie, the granite area, the Carboniferous area, the Red beds prairies, the Staked plains, Toyah basin, and the Stockton plateau; the south plateau of the Rocky mountains, embracing isolated mountain masses and cañons, grass plains, and bolson deserts.

PLANT FORMATIONS.

The classification of plant formations employed in the following pages is based chiefly upon local conditions of soil, geologic structure, and physiographic features, that is the formations are edaphic. For example, rock formations, forest formations, and salt basin formations exist because of local soil structure or content. In the case of grass formations, climatic factors, especially moisture, play an important part, not only in determining the existence of a grass formation as opposed to a forest formation, but also in determining the special association of species in the different formations. For example, although the physical structure of the Staked plains is most favorable to forests, such formations are naturally excluded by scantiness of rainfall; and in the Rio Grande plain the pigmy forest of chaparral succeeds the dense mesophytic forests of the Atlantic coast plain because the factor of moisture has suffered so great reduction. In every case the particular type of formation existing upon a given local area depends upon the local conditions of physiography and geology. For example, of the forest formations the post oak type is always present upon sand and gravel beds. The streamway cañon, hill bluff, and escarpment forests are all products of the soil conditions prevailing where they occur; for, although their differences are due to differences

of moisture, these are a result of the physiographic and geologic peculiarities, and may occur independently of rainfall and humidity.

The plant life of the region in general may be included in the following formations: (1) grass formations, (2) woody formations, (3) succulent formations, (4) rock formations, (5) halophytic formations.

I. GRASS FORMATIONS.

The consideration of plant formations in western Texas may begin appropriately with the grass formations, for, excepting only the highest mountain summits of trans-Pecos Texas, the climate is a "grass plains climate," and the grasses may be said to form the matrix of the vegetation of the region. Texas is thought of commonly as a land of grasses, and properly so as regards the portion considered in this paper. Under what may be called natural conditions, to distinguish them from conditions which prevail under the present era of exploitation, the grass formations held their own in the perpetual struggle against woody vegetation. With the advent of the cattle business, however, this advantage was lost, and the present is an era of the rapid encroachment of timber formations. These phenomena and their causes will be specially considered in a subsequent paragraph. Mention is made of the matter here to explain that in discussing the grass formations as they now exist we are dealing with a vegetation which, though still the dominant type, has not only a more restricted distribution than formerly, but is undergoing perceptible changes, not only in restriction of its area as the dominant formation, but in the association of species within the formation.

Along with the grass plains vegetation will be discussed those types of formation which, though distinct enough as formations periodically, never for more than a brief period form the dominant vegetation, and are in every case distinctly a prairie feature. Such are the prairie annuals (generally mesophytes) and the lignescent perennials (tropophytes).

In the present discussion the formations are taken up by geologic and physiographic provinces, because they seem not to be distinguished so much upon floristic as upon ecologic grounds. Temperature conditions will be seen to paly a rôle as between a province in the extreme south and one in the extreme north, but even then chiefly in the floristic content of the annuals and lignescent perennials of the prairie formations. Again, the breadth of area from east to west, following the lines of decrease in rainfall, gives the grass formations of the eastern provinces a physiognomy differing from that of the extreme western. Finally, as previously mentioned, since edaphic factors exert such a marked control upon formations, the consideration of the grass formations by provinces will give the full force of these factors.

A preliminary word may be said in reference to the grass formation of the region as a whole. It was stated above that the climate of the region is a grass plains climate, and that the grasses form the matrix of the vegetation, this being true even where they are not the dominant element. Taking the region as a whole, there is a wide range of climatic (hydrometeoric) conditions between the east and west boundaries. But even in the province of greatest rainfall, climatic conditions, together with geologic and physiographic conditions, result in a decidedly xerophytic vegetation. The grass vegetation is the chief exponent of the xerophytic conditions, and certain ecologic types of grasses are found through the entire region, as *Bulbilis dactyloides*, the specifically designated "buffalo grass." Throughout the entire region, also, the dryness of air and brilliancy of sunshine cause adaptations to rapid transitions from active growth to dormant conditions, great quantities of nutritive materials being stored in the dormant parts.

THE RIO GRANDE PLAIN.

PHYSIOGRAPHY AND GEOLOGY.—The area here included in the Rio Grande plain is really the continuation of the Atlantic coast plain west of the 98th meridian. It is in general a triangle,

whose vertices lie at San Antonio, Del Rio, and Brownsville. At the north, along the base of the triangle from San Antonio to Del Rio, the plain ends abruptly at the southern margin of the Great plains region, which is here marked by a sudden downfall, the Balcones fault escarpment, which here has an altitude of about 1000 feet. From the foot of this escarpment the plain slopes gradually to Gulf level. The Rio Grande plain of geologists, called also the Rio Grande embayment, is described as a constructional plain lying between this escarpment of the plains and the east front of the Mexican cordilleras. Its surface consists of the sheet flood débris of these two border regions, and its individuality, as distinct from the Atlantic coast plain eastward, lies in its construction and its surface weathering under far drier conditions than those which prevail eastward.

The sheet flood débris from the margin of the plains does not cover all of the Rio Grande plain as here defined. The flat coast prairie with its compact clay structure still extends along a narrow belt toward the lower Rio Grande. From Brownsville northward to the middle of the region extend vast sand plains, tongues of which reach well up toward the escarpment border. The flood débris lies in coarser or finer beds over the northern half of the plain, with exposures of arid clays, flat silt plains, or ridges of coarse gravel. Add to these features the basalt extrusions both along the northern margin and in the southern sand plains, and the streamway erosions through the various deposits, and we have the factors which not only combine to determine different types of grass formation, but have also figured prominently in favoring the encroachment of the woody vegeation, chiefly the chaparral formations.

CLIMATIC CONDITIONS.—The temperature conditions are of great significance to vegetation in this province, but only indirectly do they react upon the character of the grass formations. This indirect control consists chiefly in permitting the occurrence of woody species that require high annual temperature (Mimoseae for example), which, with certain artificial barriers removed, the burning of the grass notably, are capable of

waging a successful struggle against grass vegetation. A further result of temperature conditions upon the grass formation is to determine, in conjunction with moisture, the floristic content of the subordinate elements in these formations — the mixture of annuals and lignescent perennials with the grasses.

With regard to moisture conditions in general, scant rainfall, low humidity, and brilliant sunlight, are such as to give the grass vegetation a pronounced xerophytic structure. In this respect the grass formations agree with those of the dry plains westward, in which, with the approach of the resting period, coincident commonly with rainless periods, the aerial parts become "cured;" that is, they die, retain without loss their nutritive qualities, and remain in a good state of preservation.

Since the 98th meridian is a mere arbitrary boundary, selected with reference to separating approximately the xerophytic vegetation regions from the mesophytic, it is evident that at the eastern border of the Rio Grande plain, especially in the coast region, the grass formations approach more nearly the mesophytic structure; while at the west, along the Rio Grande, they approach the pronounced xerophytic aspect of distinctly arid regions.

With respect to the relation of grass formations to woody formations in the Rio Grande plain, the encroachment of the latter has been so vigorous as practically to destroy continuous areas of open grass formation. Much of the province is covered by impenetrable thickets of chaparral. There are broad stretches of savanna where the grass formation is more open, but the areas are studded with isolated individuals or clumps of live oak, or by open post oak formation.

On the basis of geologic structure and soils, three types of grass formation may be distinguished: (1) those of the flood débris plains; (2) those of the sand plains; and (3) those of the coast prairie. The first two are by far the most extensive and important. The third is but a slight extension of the coast prairie formation which is so characteristic on the Gulf coast from central Louisiana westward to our region.

THE FLOOD DÉBRIS PLAIN.—The flood débris from the Cretaceous formations of the Edwards plateau covers approximately the upper half of the Rio Grande plain, the altitude being from 500 to 900 feet. The level stretches of this part of the plain are covered with finer silt débris, the mesquite-chaparral plains. There are arid clay hills in the Eagle pass region, and coarse gravel and stony slopes nearer the escarpment, besides basalt cones or ridges and the outlying block of rough hills (Anacacho mountains).

Floristically the grasses are chiefly of genera making up the buffalo grass range of the plains northward. On the rougher areas, especially westward, the extreme xerophytic conditions give the aspect of the arid plains. The associated species are chiefly lignescent perennials, or perennials with thick fleshy or tuberous roots, such as *Jatropha spathulata sessiliflora* on stony or gravelly soil, *J. macrorhiza* on loose silty soil, and numerous other Euphorbiaceae and Nyctaginaceae peculiar to warmer lower Sonoran areas.

The grass formation on these areas has been very much reduced by over-pasturage, so that during drouth periods vast tracts lie quite bare of grass vegetation. In this condition pastures not wholly beset with chaparral have the appearance of fields lying beaten and fallow. So great has been the depletion of grasses that during certain dry years it was stated that from fifteen to twenty-five acres of land were required to pasture a single cow. What permanent effects on the grass formation will result upon areas so denuded it is not yet possible to say, except that the chaparral will cover the entire plain. The grasses have great recuperative power, and it is said that after periods of abundant rainfall the earth is covered again with a close grass formation. No doubt a period of rest from excessive pasturage would enable them to recapture fully much lost ground. Of course, with the presence of the chaparral and the new relations it involves, the original grass formation of open sunny plains will suffer some material changes. This subject offers a field for special investigations.[6]

[6] SMITH, JARED G.: Grazing problems of the southwest. Bulletin 16, Division of Agrostology, U. S. Department of Agriculture. 1899.

THE SAND PLAINS.—These sandy grass plains constitute the most considerable feature of the southern half of the Rio Grande plain, and arms from them reach well toward the northern boundary. In some areas the sands are so deep and shifting as to render any stable vegetation impossible. Such areas are not yet well enough known to discuss here. The conditions as regards earth moisture in the sand plains are such as to leave them covered with grass vegetation and accompanying herbaceous plants when the flood débris plains are bare of the corresponding formation. This is because they are not only better receiving areas, but the underground water is more available, for as the altitudes are low the distance to water is not great, and the open texture of the ground aids in that short distance in bringing water to the surface vegetation.

The grass formations of the sand plains are different from those of the flood débris plains in two important respects; first in the more open character of the formation, and second in their floristic content, in which the secondary elements — the prairie annuals and lignescent or succulent perennials — are especially involved. The open character of the grass formation permits an uncommonly varied growth of sand plains species. Many of the more important of these are of semitropical affinities, and hence not found in the more northerly or more elevated provinces.

THE COAST PRAIRIE.—This is typically a sod prairie with grasses and sedges of mesophytic requirements, and annuals similarly adapted to wet, low, coast lands. Such prairie is continuous between Houston and Corpus Christi, except for streamway interruptions; though in passing westward along the line of decreasing rainfall the formation gradually becomes of xerophytic stamp, and the semi-marsh land species are succeeded by grasses of the plains. Within the province of the Rio Grande this formation passes into that of the sand plains.

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[*To be continued.*]

A STUDY OF THE SPORANGIA AND GAMETOPHYTES OF SELAGINELLA APUS AND SELAGINELLA RUPESTRIS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XXXI.

FLORENCE MAY LYON.

(WITH PLATES V–IX)

SELAGINELLA APUS.

SPORANGIUM.—It is by no means an easy matter to determine the origin of the sporangium in *S. apus*. It is quite possible, from a number of slides, to select a series which shall seem to prove that the archesporium consists of two superficial cells originating just above the axil of a sporophyll (*figs. 3, 4*). It is equally easy to procure evidence that a single epidermal cell initiates the sporangium (*figs. 1, 2, 5*). This single cell may be either upon the sporophyll or removed by several intervening cells from its base. The exact line of demarcation between sporophyll and axis is indeterminate. The difficulty lies in the fact that until the sporangium is well established, consisting of some half dozen or more cells, there are almost no indications in the structure, or size, or staining qualities of these cells to distinguish them from the vegetative tissue. Moreover, a sporophyll originates in close proximity to a sporangium (*fig. 5*), and at about the same time and until it has established an apical cell there is no way of distinguishing it from a young sporangium. These facts render cross and tangential sections well nigh useless for an interpretation of the earliest stages. From serial radial, *i. e.*, vertical, sections of the strobilus, if cut with due reference to the phyllotaxy, it is possible to form conclusions by comparison of the series of sporangia and sporophylls in the same rank and of different ages that appear in an exact median section. It is evident that the number of such

sections which may be obtained by ordinary means is very limited. I found it necessary to imbed the strobili singly, examine each section as its plane approached the median region, and constantly alter the angle of the paraffin block in the microtome, until by the vascular strand of the axis and the leaf traces of the older sporophylls I could estimate approximately the section sought. Even with these precautions, I was not infrequently doubtful as to whether a cell that appeared in the right place theoretically for an archesporium might not be the initial cell of a sporophyll from the next rank that a slightly oblique section would display. These explanations are necessary, for after much painstaking study of many sections of tips of very young strobili, I find myself becoming less certain of there being a definite rule governing the initial phases of the sporangial growth. In many median longitudinal sections cut in the manner described above, a single epidermal cell projects from the surface in a vertical line between the youngest sporophyll and the apical cell of the strobilus. Occasionally it takes a deeper stain than the neighboring cells. There are usually from ten to twelve cells between it and the apical cell, and two or three between it and the subtending sporophyll (*fig.* 5). Quite as often this projecting papilla is composed of *two* cells of equal size lying in the vertical line (*figs.* 3, 4). In either case periclinal walls are formed, cutting off one or two cap cells (*figs.* 2, 5, 6). From the hypodermal cell or cells, thus formed, originates the sporogenous tissue. From the cap cell, which divides much more rapidly, the sporangium wall is formed. It is possible, I think, to determine in sporangia of various stages, nearly up to maturity, whether in a given case it originated from a single epidermal cell or from the two superimposed cells. In the second case, the complex of cells resulting from each of the two primary cells consists of more regular radial rows, and there is a quite definite plane of cleavage between the two groups. The only other interpretation of appearances like *figs.* 6 and 8 is that the primary single archesporial cell divided first anticlinally, thus producing the superimposed cells, each of which then cuts

off a cap cell. I have sought in vain, however, to establish that the first two are sister cells. When the sporangium consists of from four to six cells (*figs. 6, 7, 8*), the hypodermal cells assume a different appearance when stained, which distinction is maintained thenceforth in the development, and establish their identity as primary sporogenous cells. There is no apparent regularity in the order or plane of their division, with the exception above stated. The tapetal cells are differentiated very early in the history, and are the peripheral sporogenous cells which assume a more symmetrical shape and regular arrangement (*fig. 10*). A few of the cells in this layer, lying directly above the pedicel of the sporangium, appear to be derived from the vegetative cells in that region, and are not the lineal descendants of the archesporial cell.

Simultaneously with the differentiation of the tapetum the sporangium wall divides into two layers by anticlinal partitions (*fig. 10*). The outer layer soon surpasses the inner in the size of its cells (*fig. 11*). A pedicel develops by the multiplication of the sterile cells next to the axis and beneath the sporogenous mass. The megasporangium cannot be distinguished from the microsporangium until the moment when the cells of the sporogenous tissue cease to divide, separate from one another, and float in the sporangium. At this period, if one or two cells are more regular in form, stain more deeply, and possess a larger nucleolus, they are megaspore mother cells (*figs. 13, 35, 36*). The microspore mother cells are not distinguishable until the karyokinetic figures develop that precede their division into spores. A comparative count of the microspore mother cells in this stage and the cells in a corresponding megasporangium indicates that there is at least one more period of cell division in the former than in the latter. A cytological study may determine other means of identifying the two.

MEGASPORES.—The megaspore mother cell becomes nearly isodiametric, enlarges, stains deeply, and lies near the tapetum (*figs. 13, 35*). Apparently the mother cell never originates far within the sporogenous tissue but always near its periphery.

Infrequently two mother cells occur, and these may go through all the later stages of development, thus forming eight spores in a megasporangium. Normally the membrane of the single mother cell becomes distended by the imbibition of fluid that has been poured into the sporangial cavity from the tapetum. Two successive divisions follow each other with great rapidity. The spindle of the first division I have seen but a few times; the two that follow, I saw more frequently (*figs. 16, 17*). These are extremely small and delicate, occupy the middle of the cell, and are soon much obscured by fibers which arise in the surrounding protoplasm. These fibers at first radiate in all directions from no definite center, but later assume the form of a sextuple spindle with the four daughter nuclei at the poles. No cytological work was attempted, beyond determining the method by which the spores originate, but it is evident even from a cursory examination that there is some connection between the enveloping spindle fibers and the two lumps lying against the nucleus which are represented in *figs. 11, 13, 15*. In the meantime there has appeared a new membrane just within the mother cell wall (*fig. 15*). It is very delicate, but of unequal thickness, and can be detected only in particularly fortunate sections. Whether this membrane arises by cleavage from the mother cell wall, or *de novo* from the protoplasm of the cell, is necessarily a matter of speculation in an object so small. Nuclear plates form across the spindles, and the mother cell divides into four spores tetrahedrally arranged. At the moment of their separation the nuclei lie near the bases of the spores, which correspond in position to the poles of the sextuple spindle, but soon move toward the apices (*figs. 16–18, 22*). As the spores increase in volume, by their pressure outward, and by a folding inward on the part of the irregularly thickened special mother cell membrane above described, the tetrad presents the appearance of a four-lobed body surrounded by a single envelope whose continuity is not broken, floating in the fluid that fills the distended spore mother cell membrane (*figs. 17–19*). Either the special mother cell membrane itself thickens, or a new coat is

formed upon its inner surface. This is the exospore (*figs. 20–22*). The spores increase in volume, but the exospore expands so much more rapidly than does the protoplasmic content, that the latter is left in the apical portion of the spore cavity as a tenuous spherical vesicle of protoplasm filled with a limpid fluid (*fig. 37*). A single very small nucleus, in which with difficulty may be seen one or two nucleoli, lies in the region nearest the spore apex. The rest of the spore cavity between the vesicle and the exospore is filled with a limpid fluid of the same nature as that which occupies the space between the tetrad and the mother cell membrane. Soon hair-like radiations appear traversing these fluid regions (*figs. 42, 43*), whose general direction is from the spore mother cell membrane toward the center of the tetrad. A thick layer which stains very deeply appears upon the inner face of the exospore (*fig. 37*). The latter maintains its more rapid rate of growth and soon afterward is widely separated from this layer by a space filled with the liquid and the radial fibrillae (*figs. 38, 42*). The sculpturing of the exospore begins almost immediately upon its inception. The spines are laid down by depositions of matter derived from the liquid between the exospore and the mother cell membrane (*figs. 42–46*).

As the megaspores increase in size, they are forced apart by the liquid in which they float seeping in between them (*figs. 38, 42, 43*) and the exospore is ruptured between the spores in such manner that each presents the appearance of a tetrahedron with a hemispherical base and three plane triangular faces. The tearing apart of the spores leaves a trefoil-shaped cleft extending from the apex along the three ridges between the triangular faces, and bounded by the flaring flaps of the torn exospore (*fig. 58*).

The sterile mother cells in part disappear by dissolving in the slimy fluid in the sporangium cavity, but not until the exospore is well developed. Some persist however throughout the development of the gametophyte and perhaps may grow slightly; they never divide.

FEMALE GAMETOPHYTE.—The spore is but a small fraction of

its final volume when the sexual generation begins, thus overlapping the asexual (*fig. 44*). The initial steps of the female gametophyte development are the rapid expansion, without corresponding increase in thickness, of the protoplasmic vesicle, and the division of its nucleus. The nuclei divide by karyokinesis, and with each successive division become larger (*figs. 45, 46*). The thick envelope surrounding the vesicle stretches, becoming proportionately thin as its surface increases, until it comes to lie against the inner surface of the exospore. At this stage it consists of two distinct layers, the endospore and mesospore, both mere films which may be readily detected, as they stain differently and are easily torn apart (*fig. 46*). The gametophyte at this stage thus consists of (1) exospore, still growing, (2) mesospore; (3) endospore; (4) the protoplasmic vesicle, consisting of a very thin and homogeneous layer of protoplasm applied to the inner surface of the endospore, in whose apical region are imbedded numerous large, ovate, flattened nuclei; and (5) a large central vacuole filled with a watery fluid in which are suspended many oil drops.

Beyond the increase in the number of nuclei, which preserve about the same relative distance from one another, there is no further change until the spore membranes complete their growth. When the maximum size is reached, fibrillae arise in the protoplasmic vesicle at the apex, and radiate downward over its surface, blocking it off into irregular areas, each of which contains one or more nuclei (*figs. 49, 51, 52*). Simultaneously the protoplasm becomes invaded with masses of granular matter, and encroaches on the space occupied by the vacuole. Nuclear divisions take place radially, and so rapid is this process that frequently the spindle fibers of three and four generations of nuclei may be seen in a single section. The fibrillar radiations permeate the protoplasm, keeping pace with its increase in thickness. As the central vacuole diminishes in size, its contents change in appearance from an emulsion to a turbid fluid thickened with granules (*fig. 53*). The protoplasmic fibrillae apparently are concerned with the distribution

of this nutriment before cell walls are formed. They have the appearance of streams bearing granules. The final and penultimate divisions of the nuclei are distinguished by the appearance of nuclear plates and spindles of quite different appearance, which result in the formation of definite cells with cell walls, each containing a single nucleus (*figs. 26–28*). At this stage, each nucleus is so surrounded by a mass of proteid as to be completely obscured. The only cells not thus gorged are a limited number which lie in the upper layer nearest the apex, beneath the trefoil-shaped cleft in the exospore (*fig. 54*). By continual multiplication they form a prothallial cushion, which widens the breach and bulges through. These cells are much smaller than those filled with the food supply. There may be from three to five layers in this cushion. There is no diaphragm between the region designated the prothallial cushion and the mass of storage cells underlying it.

ARCHEGONIA.—A few cells in the prothallial cushion soon become conspicuous by reason of their large nuclei. Each divides by two periclinal walls, forming a tier of three cells. The uppermost of these divides by two anticlinal walls at right angles to each other into four cells. These again, by periclinals, form the four cover and the four neck cells. The middle one of the original tier does not divide and becomes directly the single neck canal cell. The lowermost divides into the egg and the ventral canal cell (*figs. 29–32*). A suggestive irregularity sometimes occurs in the last mentioned division. The central cell, that is, the lowermost cell of the original tier, may divide in such fashion that the egg and its sister, the ventral canal cell, may lie side by side in the venter of the archegonium, instead of in the normal fashion of ventral canal cell above the egg (*fig. 32*). The cover cells project very little from the surface of the prothallium. Thus the archegonia are imbedded in the surrounding tissue, whose cells in immediate contact with the egg and the ventral canal cell become more or less modified in form. The neck canal cell pushes up like a wedge, spreads apart the four neck cells, and dissolves. The ventral canal cell

also disappears (with a possible exception noted hereafter), and the egg lies free in the venter. There is a large receptive spot on the oosphere, and its nucleus is not centrally placed (*fig. 33*). I have never seen more than five archegonia in a single gametophyte.

FERTILIZATION.—Not only are the archegonia formed in the unshed spores, but frequently, at least, fertilization and the early phases of the sporophyte development take place while the sporangium with its prothallus are still in the strobilus. The strobili cease to grow, fade, and may separate from the plant before fertilization, but the spores do not fall from the sporangium. It was not until I had collected from the soil several hundred spores which had been shed, with the expectation of finding fertilization stages, that I thought to examine the withered strobili. Almost without exception in these I found embryos, whereas *in no case* have I found any evidence of fertilization in the spores that are shed.

FURTHER DEVELOPMENT OF THE MEGASPORANGIUM.—The glandular tapetum is very active until the megaspores have stored their maximum amount of nutriment for the growth of the embryo. At this stage they quite fill the sporangium cavity, which in consequence has assumed a four-lobed appearance. The tapetum then declines in importance. Its cells collapse and form a pavement-like layer. The outer layer of wall cells becomes greatly modified. In section it appears precisely like a similar section of the annulus of a leptosporangiate fern (*fig. 52*). Four areas of the larger thick-walled cells, corresponding to the protuberances caused by the spores lying within, are separated from one another by narrow strips of small cells with thin walls. The latter are the lines of dehiscence. The sporangium splits into two valves along these lines, but the halves do not separate so widely as to allow fertile spores to escape. Apparently they may open and close more than once. The sporangium appears fresh and active, and its wall contains chlorophyll until after fertilization has occurred. With the decline of the tapetum the lower stratum of the wall becomes

more vigorous, as does a group of cells that lies just above the pedicel, and which projects into the sporangial cavity (*fig. 58*). This cushion is in close relation to the vascular strand and probably facilitates the supply of nutriment to the sporangium wall, until the embryos begin to form.

Frequently I have found microspores (in which the spermatozoids had formed) within the megasporangium at the period of fertilization, and it is possible that the microspores are hurled into a gaping megasporangium when ejected from the microsporangium.[1] This is rendered more probable by the frequent occurrence of microspores caught in the angles between sporophylls and stem. Moreover, if plants that have become somewhat dry be profusely watered, the mature microsporangia open explosively and discharge spores.

MICROSPORES.—The microspores of *S. apus* are much smaller than those of *S. Kraussiana* and *S. Martensii*. They early develop a pebbled, thick exospore, which causes much trouble in imbedding and sectioning (*fig. 69*). Moreover, a comparatively small number, in proportion to the immense output, mature. Curious aberrations in growth are constantly found. It was necessary to study mature gametophytes discharging spermatozoids and trace back the different stages to the mother cells. Frequent comparative measurements finally afforded a clew to detecting abnormalities in the early stages.

Not more than five sixths of the potential mother cells divide into spores; the others rapidly disappear. The division is accomplished in a manner analogous to the division of the megaspore mother cell, which is very little larger. Two spore coats develop, a thick spiny exospore, and the delicate membranaceous endospore. The microspores are shaped like the

[1] I have examined *S. Martensii*, *S. Kraussiana*, and *S. denticulata*, growing in the greenhouse, with reference to this point. The two former do not shed their strobili, and I have found loose megaspores containing sporophytes in the soil on the benches where the plants are growing. The last mentioned species, on the other hand, sheds its strobili in profusion. I find, however, that their spores are invariably sterile and aborted, and therefore am unable to form an opinion as to whether this shedding is the normal habit, or due to cultivation in an unnatural environment.

megaspores, but, unlike the latter, separate from one another as soon as the exospore develops. As was the case with the female gametophyte, the sexual generation begins before the microspore has ceased growing. At the moment that the microspores separate from one another, each possesses a thick and a thin coat, a layer of protoplasm parietally placed, with one nucleus, and a central cavity filled with fluid (*fig. 68*). The nucleus increases in size and divides. This process often takes place in that part of the spore where one of the lateral ridges meets the hemispherical base (*fig. 78*). The protoplasm increases in quantity and encroaches on the central vacuole. Granules of various sizes make their appearance in the cavity and in the surrounding protoplasm. These bodies stain precisely like the nuclei and the more regular ones may be mistaken for them, as I frequently discovered in the early period of my own work (*fig. 77*). By precautions in decolorizing, the presence of nucleoli always distinguish the nuclei from the granular masses. These bodies are formed by the agglomeration of many smaller granules. One of the nuclei formed by the first division remains against the wall. It may grow larger and the protoplasm immediately surrounding it is somewhat denser, but no wall separates it from the rest of the spore. This may be the vegetative prothallial cell (*figs. 70, 75*). The other nucleus passes into the center of the spore. The protoplasm that envelops it sends out radiating processes that incompletely divide the spore cavity into irregular chambers, each of which is filled with granular masses of various sizes and shapes (*figs. 76, 80, 81, 83*). These strands of protoplasm are continuous with a thin layer in contact with the endospore. The central nucleus with its envelope of protoplasm divides into two cells which usually separate from each other (*figs. 79–83*). By repeated division of each of these cells a complex results which consists of two uniform masses of sperm mother cells. There is no law of sequence which the cells follow in dividing, although the final product consists of cells very regularly arranged (*figs. 95–97*). The male

gametophyte then is made up of one prothallial cell and a naked mass of sperm cells, which later come to float in the slime produced by the disorganization of the food granules. Sometimes at this stage the large deeply stained prothallial cell may be seen flattened against the endospore (*fig. 97*). There are about 128 sperm cells. The exospore splits along the three ridges from the apex downward, and the endospore, dilated with fluid, protrudes through the gap (*figs. 98, 99*). The sperm cells separate from one another, and a single spermatozoid is organized in each. These are spirally coiled like those of Osmunda—two complete turns and a part of a third—but I can demonstrate no cilia (*figs. 33, 100*). Neither in appearance nor in movement do they resemble any bryophyte spermatozoid with which I am familiar, or have seen figured. The movement of biciliate gametes is characteristically different from that of an ordinary fern. These spermatozoids progress with a screw-like motion. The latest stages of development occur in the strobili after they are shed.

MICROSPORANGIUM.—At maturity the microsporangium wall consists of two layers of cells, of which the outer is divided into regions of thick and thin-walled cells, which enable the sporangium to open lengthwise into two symmetrical valves (*fig. 62*). The microspores are discharged with much force. If plants that have become somewhat dry are watered copiously and covered with a bell jar, the ripe microsporangia burst open and jerk back their valves, which instantly recoil and hurl the microspores. These may be seen, looking like red powder, lodged in the axils of leaves or upon any other part of the plant where they have chanced to fall. Of necessity the waste must be great. If this is the method adopted by the plant to secure fertilization it may account in a measure for the extremely small number of sporophytes that are developed.

S. apus grows most profusely in a neighboring locality, where almost daily observations have been made during the past year. Early in May 1900, when this work was undertaken, the strobili were well advanced. It was observed that if several eggs in one

strobilus are fertilized, the formation of new sporangia is checked. The sporophylls begin to decay, as finally does the axis immediately below the fruiting head. The production of new strobili went on until late in August, at which time all the strobili were shed, whether fertilized or not. In September vigorous vegetative growth took place during the fall rains, and continued until checked by several days of very cold weather in December. In the latter part of the same month, upon removing the snow that covered the plants to a depth of six inches, they were found to be green and ready to grow at any favorable moment. Large sods were lifted, without disturbing the plants, and brought into the warmth of the greenhouse, whereupon they responded promptly to the blander conditions. After a week, upon gently disentangling the individuals in order not to detach the semi-decayed strobili which were partially covered by the soil, I found several young sporophytes which had thrust their cotyledons and roots through the crevices of the megasporangia. From this it seems safe to assume that an embryo may have two periods of growth separated by one of quiescence, quite comparable to those of seed plants.

SELAGINELLA RUPESTRIS.

There could be hardly a more striking contrast in the external appearance of two closely related plants than exists between these two species of Selaginella that are natives of New England. *S. rupestris* is to be found in the most exposed situations, growing on the granite rocks on the mountain sides, wherever there has been enough weathering to insure the deposition of a little soil in the hollows. For six months of the year they endure alternate drought and drenching, and the frequent and rapid changes of temperature which are characteristic of this region, with no more protection than is afforded by their own structural adaptations. The midsummer conditions are even more trying. The plants that were studied for this work grew on bare rocks upon which the sun beats nearly all day from June to September. The fruiting spikes are to be found in profusion at all times of

the year, but, as will develop later, the spores in the main are sterile. Material was fixed first about June 15, 1900, and at intervals of two weeks thereafter until February 1901. Sods were lifted from the rocks, and planted in shallow boxes which were kept in a warm place exposed to the direct sunlight. The spores were shed freely all summer. I collected other plants from a similar xerophytic situation at Starved rock, Illinois, in August, and for comparison material was sent me in Northampton, Mass., from Austin, Texas, in November. These three regions are 800, 900, and 1600 miles apart. The plants collected in Massachusetts and Illinois, from June until February, almost without exception produced megasporangia only. The Texas material collected in November, on the other hand, was almost purely microsporangiate.[2] Expecting to find prothallia and young sporophytes developing in the spores that had been shed, these were picked out from the loam from which the plants were growing and killed at frequent intervals during the summer, with the purpose of getting all important stages. In all cases these proved to be barren. Late in August—as was the case with *S. apus*—the young sporophytes were discovered protruding from a withered strobilus that was nearly covered by the dirt. Further search produced many well-developed embryos, but it was apparently too late in the season to secure early stages (*fig. 126*).

During the first week in January, a sudden thaw was succeeded by several days of rain. Plants were collected from the mountain and gradually brought into a greenhouse temperature. The old strobili became greener at their tips, and new vegetative shoots started from the lower part of the stems. It is doubtful whether the increase in the number of individual plants in a given locality is due to any considerable extent to sexual reproduction. A hollow in the rock, or a crevice, becomes filled with a closely compacted colony that is the result in great measure of vegetative reproduction, where prostrate branches, under

[2] Some of the Texas material was submitted to Professor L. M. Underwood, of Columbia University, for identification. He informs me that it is not *S. rupestris*, but a closely allied unnamed species.

favorable conditions of moisture, have rooted, and later have severed their connection with the parent plant. In examining many colonies, very few young plants that originate from spores are in evidence, although the soil may be thickly beset with the spores that have been shed. Bits of the old plants that have been torn off by the action of the wind or rain are frequently caught in crevices along the precipices, and it is from these that new clumps are most frequently started.

In *fig. 124* I have endeavored to convey an idea of the structural adaptation of the strobilus to its austere environment. The closely overlapping sporophylls form four rows, in whose axils the sporangia have little space to develop. The growing apex is protected by at least twelve and frequently sixteen sporophylls which envelop it. The epidermis is two or three layers of cells thick on both surfaces of the sporophyll, except in a shallow groove running lengthwise along the middle of the ventral surface. In this groove are the comparatively large crowded stomata, which are protected by the next older overlapping sporophyll of the same row. While the leaves are yet very small the apex ceases to grow and becomes transformed into a branched spine. The formation of the horny epidermis proceeds from the apex toward the base. Between the ligule and the sporangium the tissue retains its meristematic nature. The vascular bundle occupies the central shaft of the strobilus, and is augmented from the apex downward by the leaf traces that join it from the sporophylls. Four large communicating air spaces, spanned by trabeculae, surround the entire system. These communicate with the exterior by certain larger chambers into which the stomata open. There is little closely compacted tissue in either sporophyll or stem. All the cells except the epidermis and the vessels contain chlorophyll. This structure is in marked contrast to the delicate unprotected sporophylls of *S. apus*.

A single superficial cell, which uniformly is so close to the base of the subtending sporophyll that it is impossible to determine whether it belongs to the stem or the leaf, is the origin of

the sporangium (*fig. 101*). The sporophyll immediately above it starts simultaneously from an exactly similar cell. A wall separates the archesporial cell into an epidermal cap cell and a hypodermal cell (*fig. 102*). The sporangium wall develops from the former, the sporogenous tissue from the latter. A few sporogenous cells near the base originate from the stem tissue (*fig. 105*).

The tapetum and sporangium development are quite like those of *S. apus*. The sporophylls and stem apex, on the other hand, have no apical cell. The ligule appears later in the history of the sporophyll than in *S. apus*, and the megaspore mother cell is somewhat larger. Certain cytological features serve to distinguish these cells from the sterile sporogenous cells (*fig. 106*). The division into spores presents some curious variations. Sometimes the spore mother cell divides once only, forming two megaspores; again, after the first division, one of the daughter nuclei may divide, or occasionally both. In any case, so far as observed, but one or two normal megaspores are ever formed; if there are others, they are dwarfed in size and never grow. That the exospore is a membrane common to both spores is evident from *figs. 119, 120, 121*. The formation of the mesospore and endospore is not preceded by any such deeply staining layer as is represented in *fig. 42*. The protoplasmic vesicle expands and overtakes the spore wall. This stage terminates the development of the megaspore (*fig. 123*). In the older sporangia, nearer the base of the strobilus in the specimens that I examined, no further development had occurred beyond increase in size and thickness of the spore coats — the contents showed that the spores were abnormal.

This sequence of events, although followed step by step repeatedly, had been rejected as probably not normal, until the sporophytes were discovered. As the number and shape of the megaspores in these sporangia which contained embryos agree with the stages described, in spite of the gap that remains to be bridged between the megaspore and mature gametophyte, it seems reasonable that the observations can be relied upon as far as

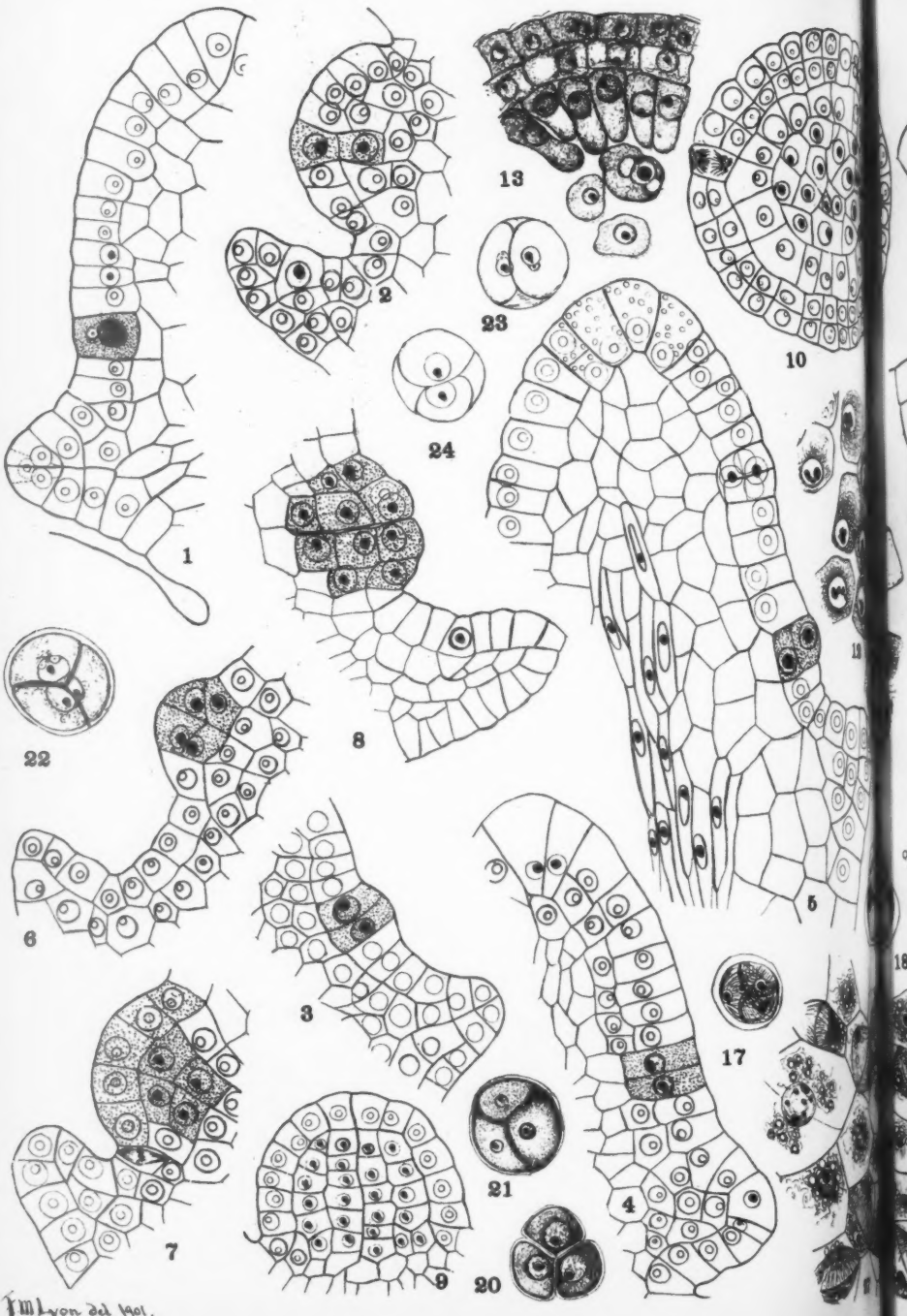
they go (*figs. 108-120*). A very close series of stages from start to finish is necessary to produce confidence in any interpretation of phases of a plant which displays so many irregularities, and evidently has so nearly lost its power of sexual reproduction.

The development of the microspores has not yet been followed in detail. Observations on this subject, together with the growth of the female gametophyte and the embryology, will be given in a future paper. One interesting feature that may be noted now is the incomplete septum which projects into the cavity of the microsporangium (*fig. 125*). This is formed in part from sterilized sporogenous tissue and in part from the cells of the pedicel.

Since the above was written, a package of fresh material has been sent me from Texas. All the plants have begun their spring growth and the winter strobili are growing at the apex. The first sporophylls of the season subtend megasporangia. I find not more than eight or ten in each strobilus. Above these are microsporangia to the number of twenty or thirty. In this material it has been my good fortune to observe the method by which the spermatozoids obtain their entrance to the megasporangia. A perfectly fresh, vigorous strobilus was cut from the plant and stripped of its sporophylls, thus exposing the sporangia *in situ*. A megasporangium, which was observed gaping open and in close proximity to a microsporangium that had discharged its microspores, was separated from the strobilus and examined under the microscope. Six microspores were caught on the sculptured surface of the megasporangium near the edge of the valves, which were slightly separated from each other. One microspore, evidently mature from the fact that the exospore was split and the endospore protruding, suddenly discharged a current of slime which at first proceeded directly away from the megasporangium. Soon, however, as if acted upon by some attractive influence from the gametophytes within, the stream turned abruptly and entered the opening between the megasporangium valves. The spermatozoids were swimming with characteristic rotary motion in this stream. With difficulty, it was

possible to make out that they were similar in shape to those of *S. apus*, but much smaller. To each was attached a vesicle. An attempt to stain them with osmic acid on the slide failed to demonstrate any more details.

ADDENDUM.— Since the foregoing was forwarded for publication it has been possible to verify the main facts and to explain certain apparently contradictory features with regard to *S. rupestris*. The spring and early summer of 1901 were extremely wet as compared with those seasons in 1900. *S. apus* growing in low pastures made few strobili and aborted spores in contrast to the profusion of the year before, whereas *S. rupestris* throve in the unusual supply of moisture and developed strobili, which in turn produced embryos prodigally. The impotency of the megaspores gathered in midsummer of 1900 was obviously due to the lack of water; for at the expiration of the rainy season this year, the last of June, and before the plants had suffered from drouth, they were lifted with all the underlying humus and placed in an open situation in the Botanic Garden. Profuse watering was continued and thorough draining secured. A large percentage of the strobili ripened after fertilization had occurred, and instead of few embryos found with much effort as in the season of 1900, hundreds of young sporophytes have been secured. The sequence of events in a propitious season, based upon the observation of two years, seems in brief to be this: Strobili are formed on the new vegetative shoots of the plant in late summer and autumn. Only megasporangia develop that season, and in these the gametophytes reached the stage bearing archegonia. In the spring, these strobili resume their apical growth, and first microsporangia appear. Thus each strobilus has a basal zone of megasporangia approximately six months old, and above it a narrow region of microsporangia. The number of microsporangia appears to be strictly limited. I have found eight to twelve as a rule. Thenceforth so long as the strobilus continues to grow during the remainder of that season megasporangia only are developed. The production of these is checked in case embryos form in the lowermost zone of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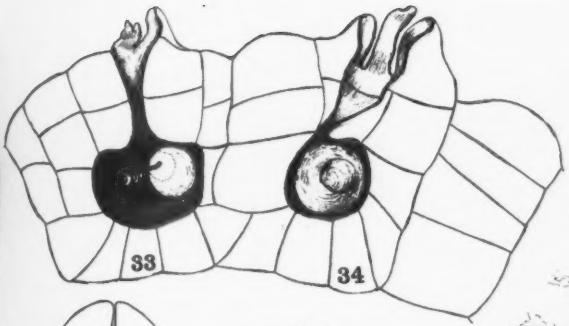

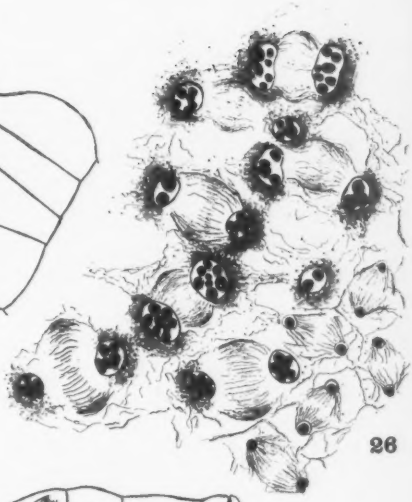

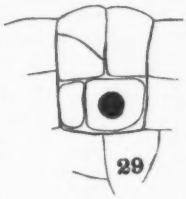

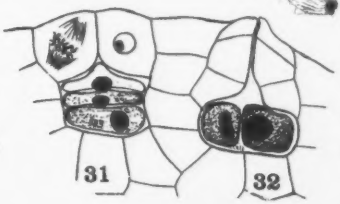

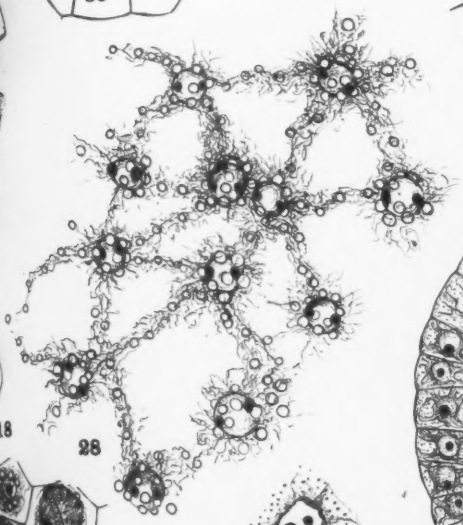

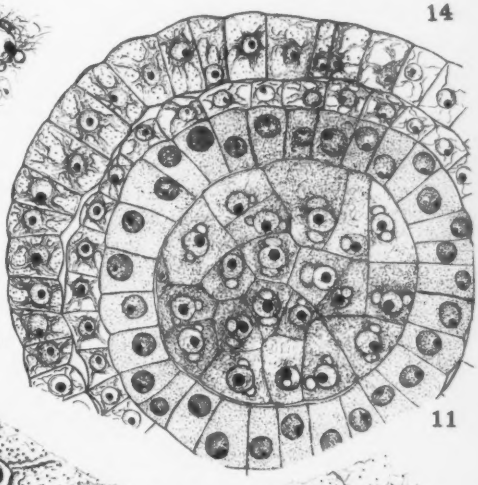

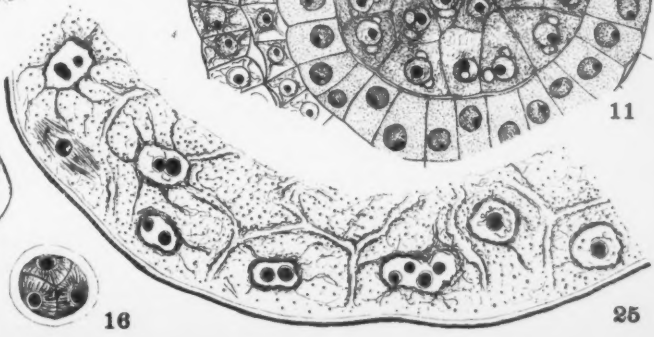

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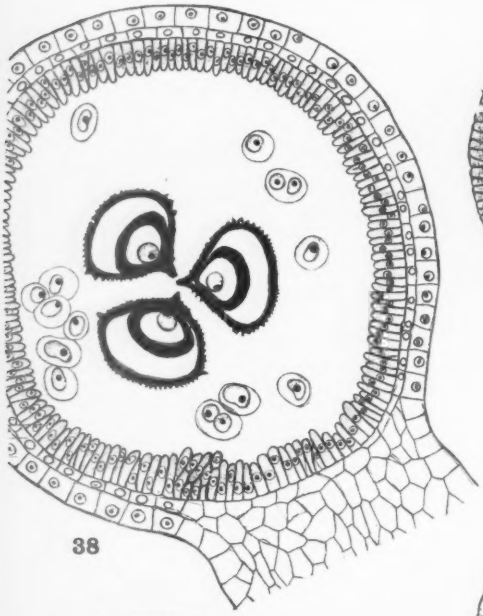

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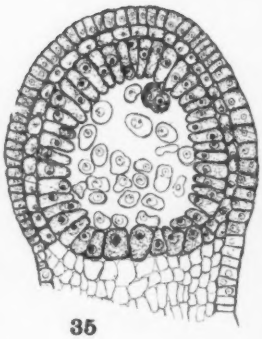

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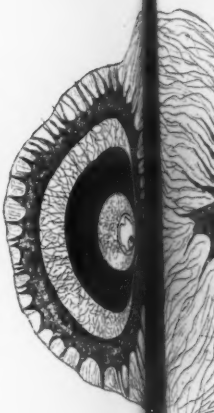

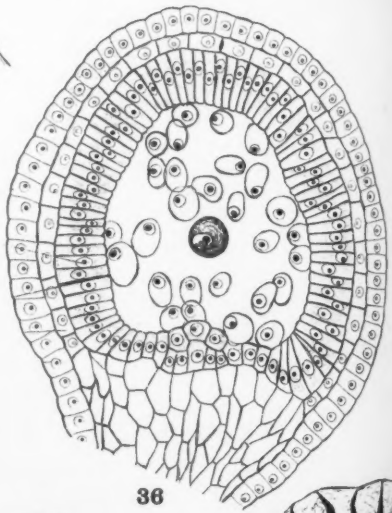

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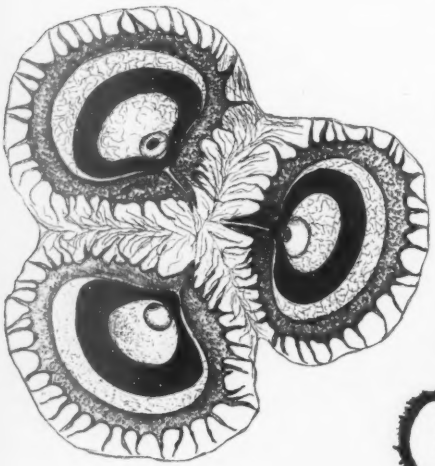

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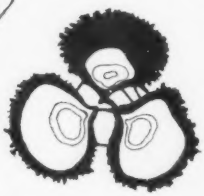

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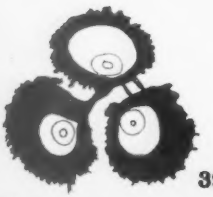

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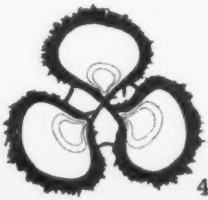

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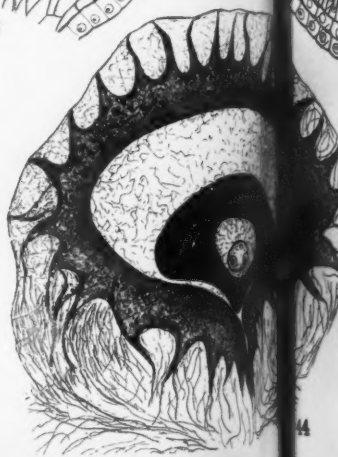

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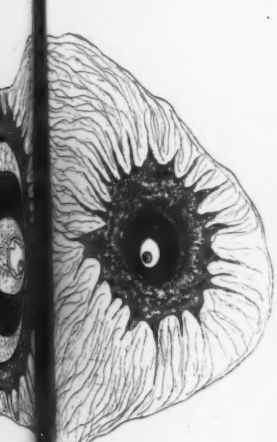

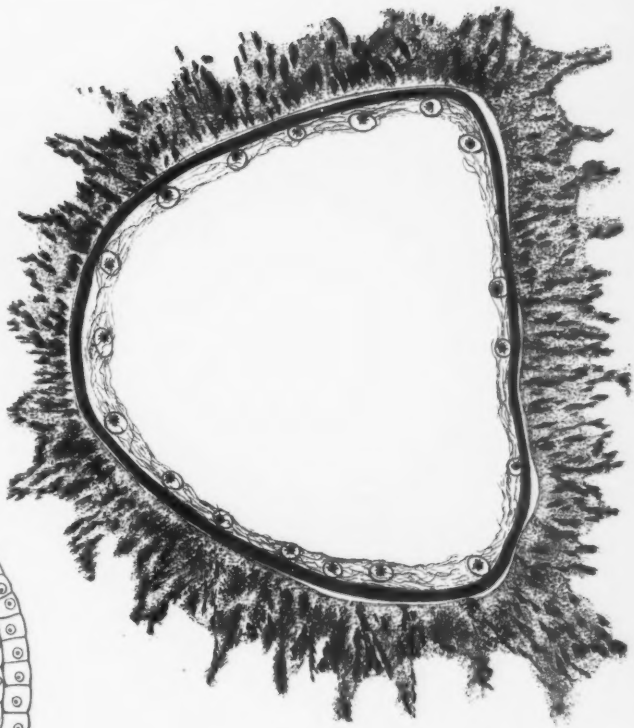

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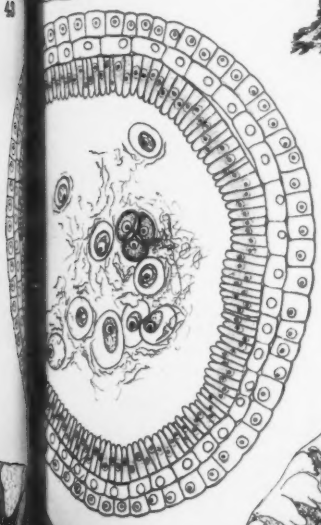

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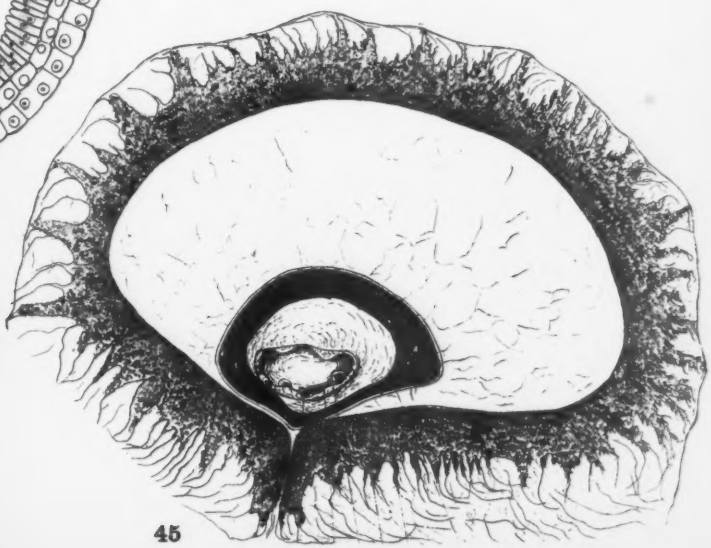

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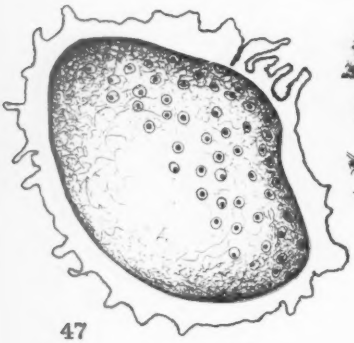

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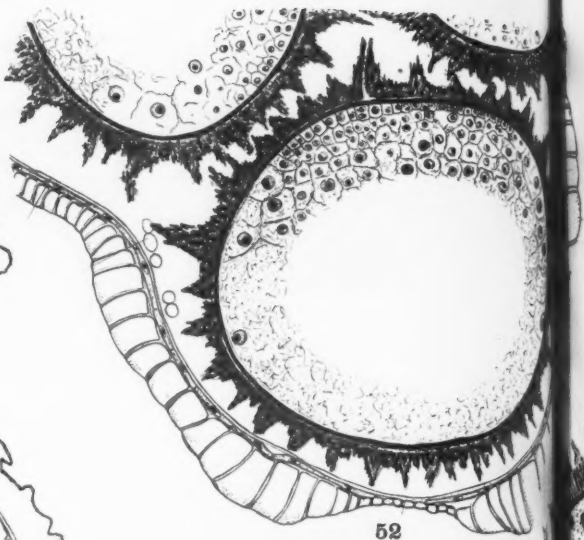

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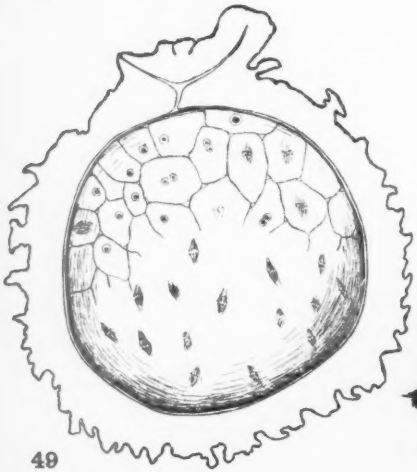

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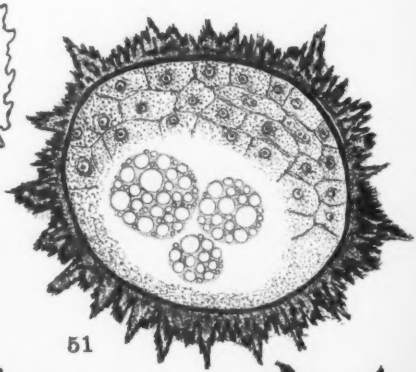

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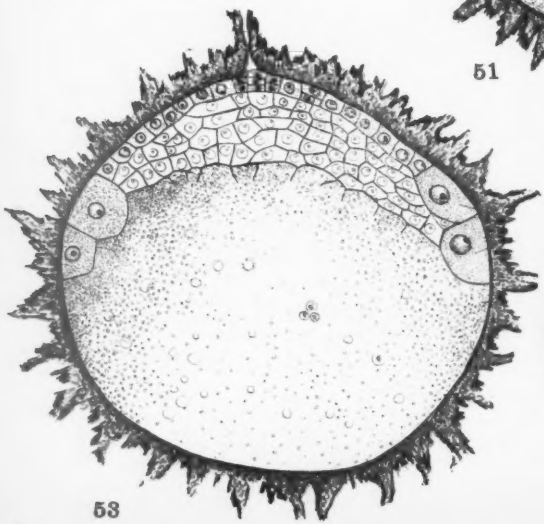

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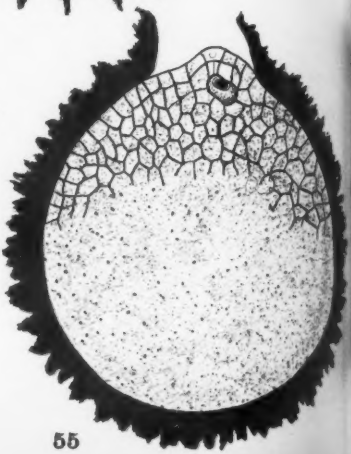

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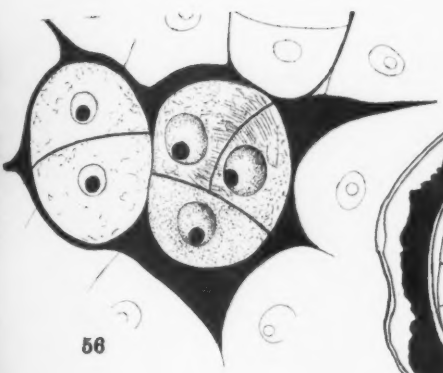

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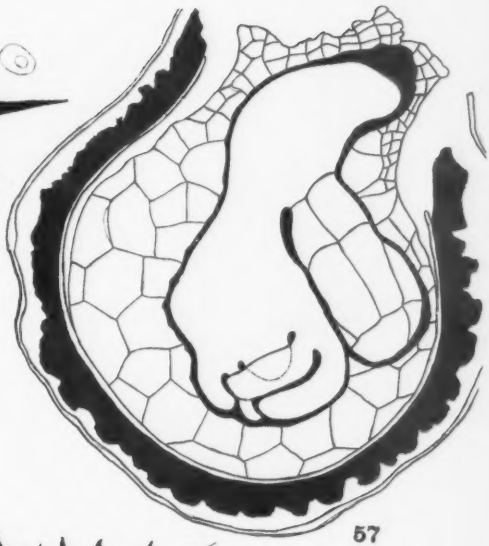

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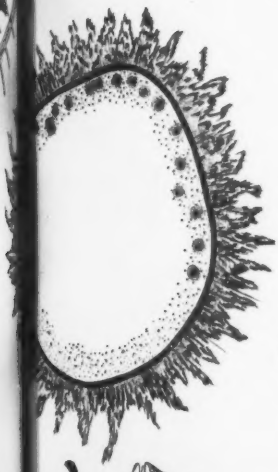

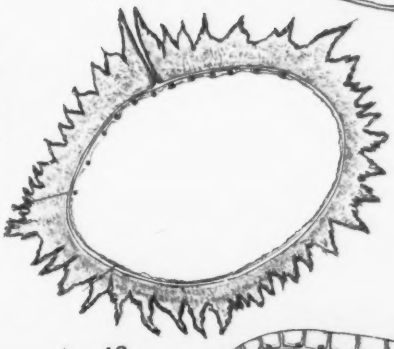

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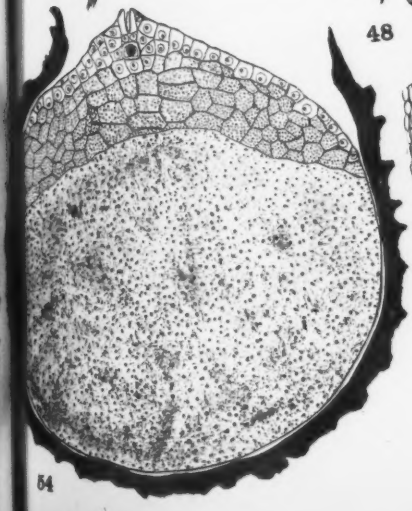

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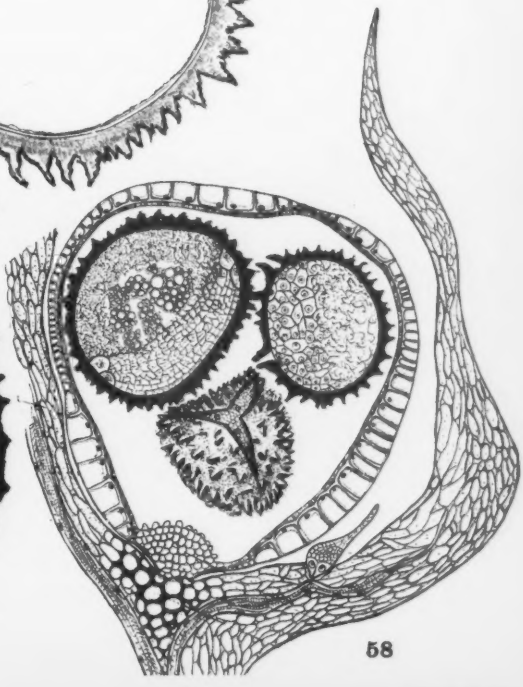

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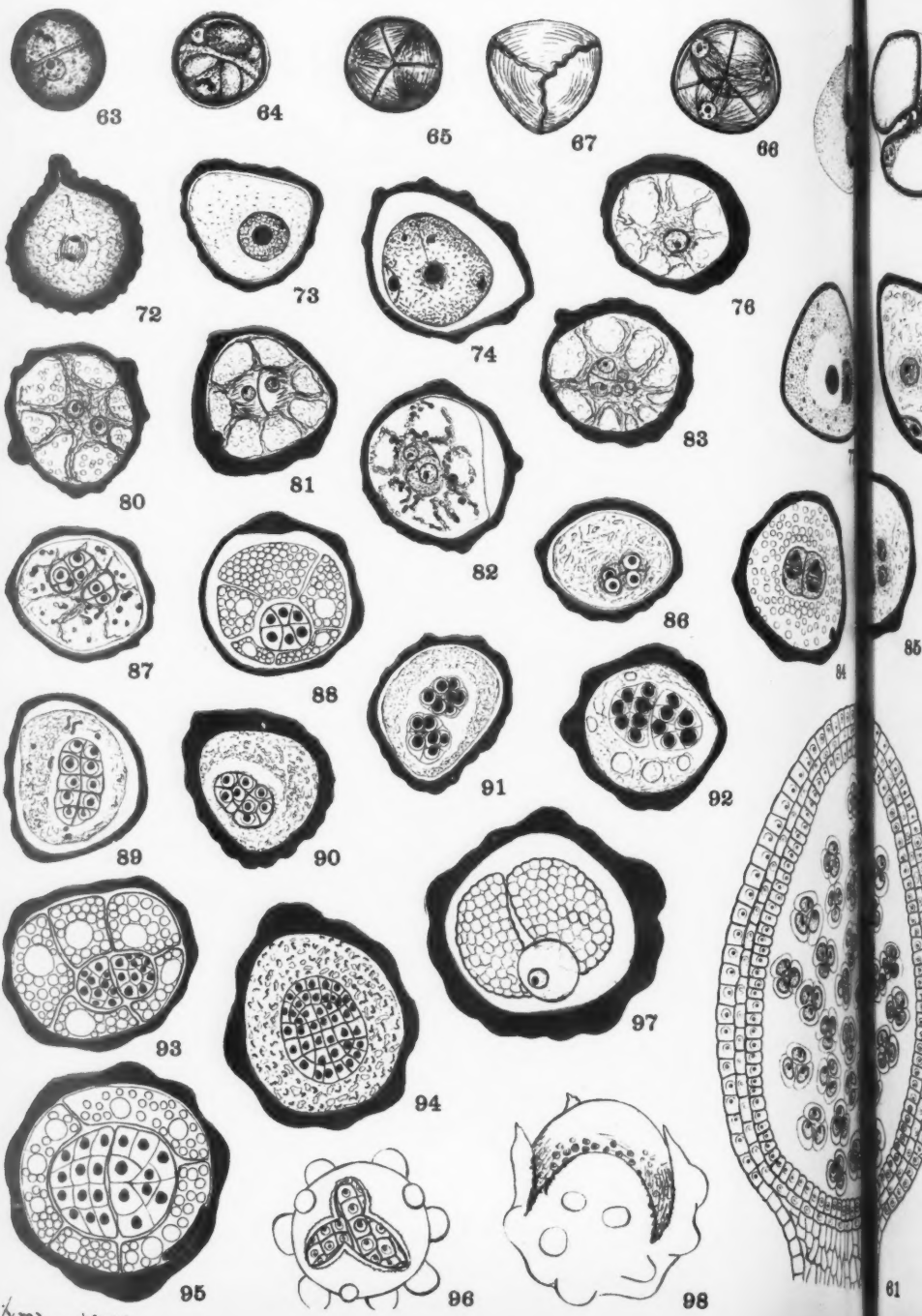
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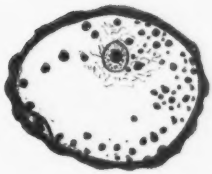
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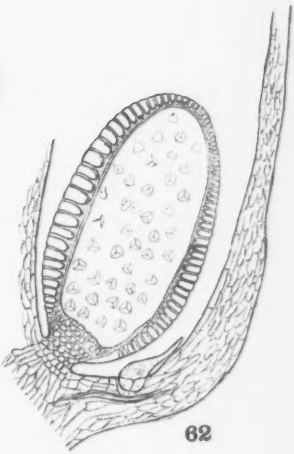
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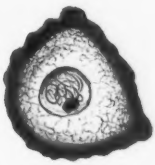
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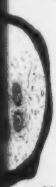
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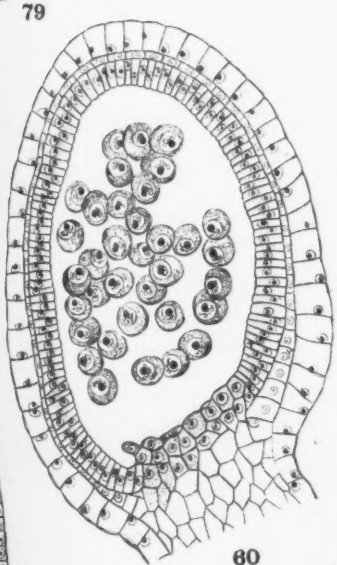
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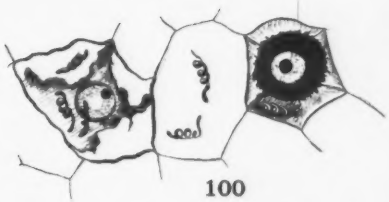
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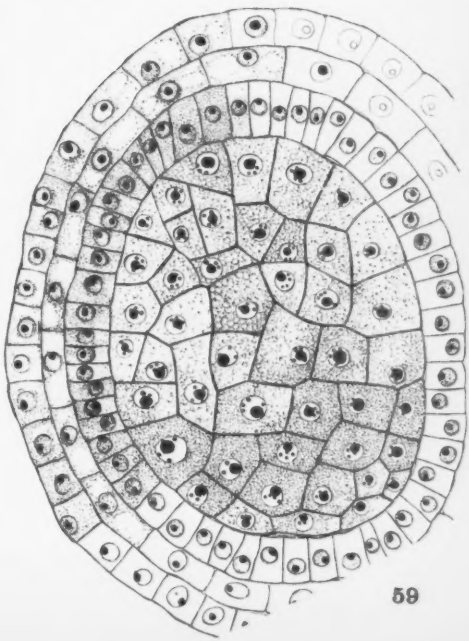
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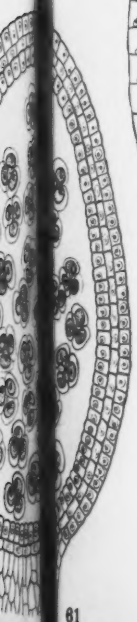
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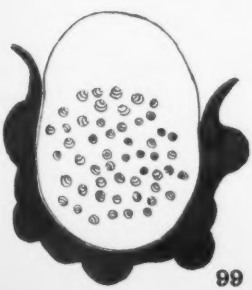
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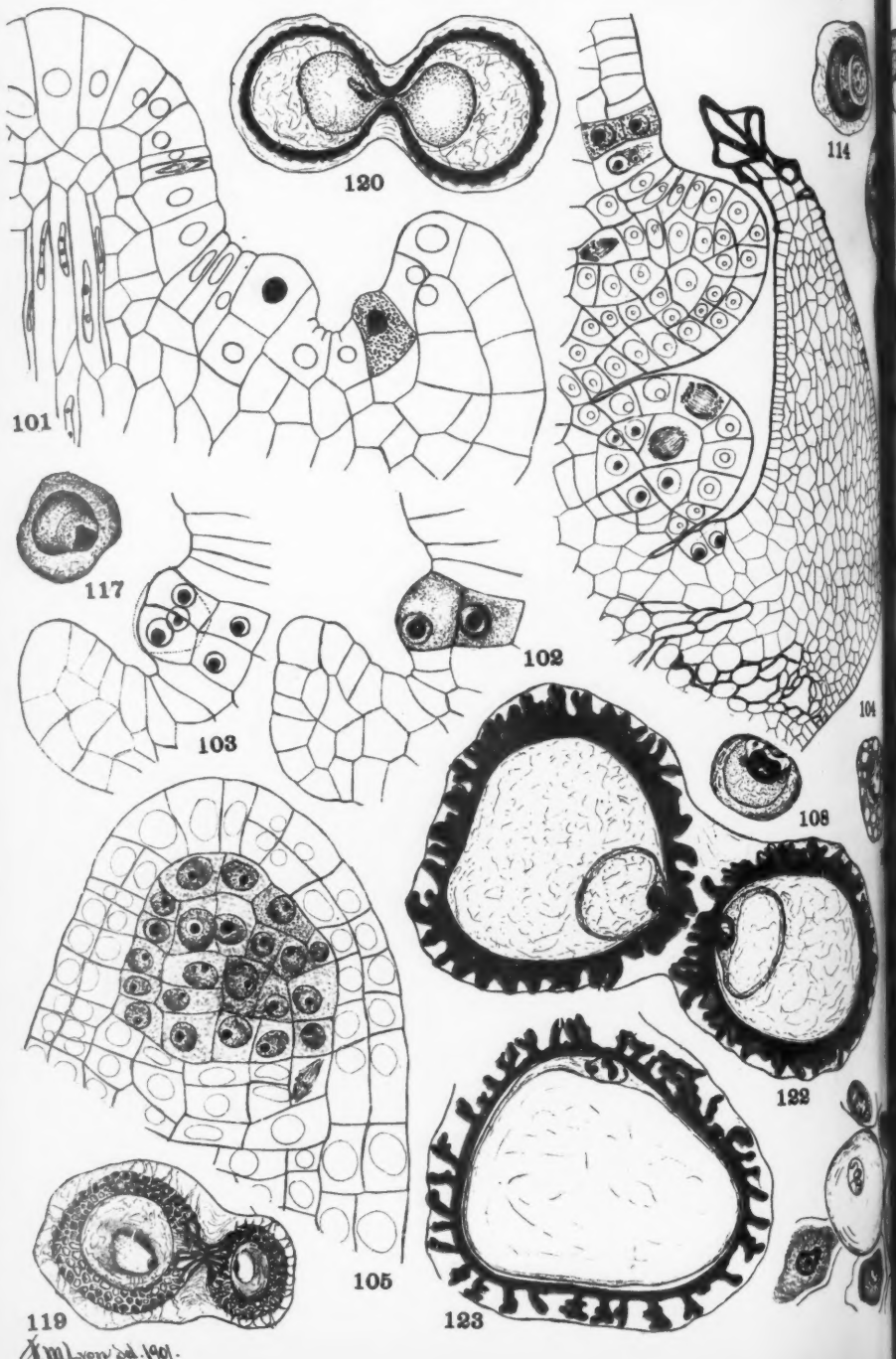
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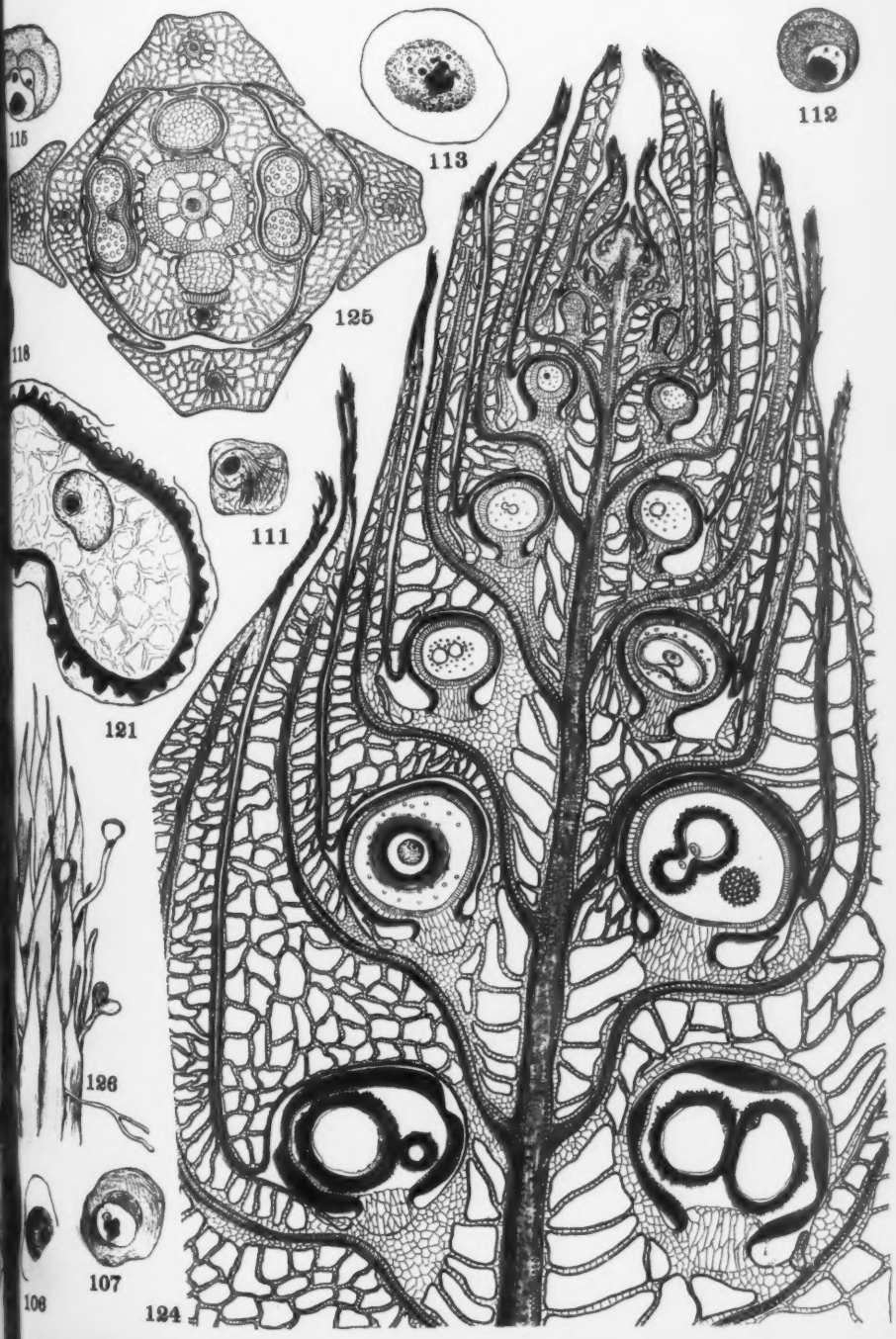

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megasporangia. Immediately upon the cessation of growth in the strobilus and during its ripening, a vegetative lateral bud on the axis immediately below the strobilus is stimulated into activity, develops horizontal branches, and roots which grow down into the humus. When this new growth is thus made independent, the axis bearing the strobilus and the germinating embryos decays, and at the period when cotyledons and roots of the young sporophytes are thrust out of the sporangia, the strobilus is lying in contact with the ground, shaded and otherwise protected by the vigorous vegetative growth that is spread above them. The strobilus decays much more slowly than the leafy axis beneath. This accounts for my finding strobili which appear to be shed from the plants. In case a strobilus fails to produce embryos, either through failure in fertilization, or probably more often because the dry season overtakes the gametophyte at a critical stage of its growth, the strobili continue to grow indeterminately throughout the season, and apparently perform the vegetative work that, under more auspicious conditions, is taken up by the new growth from the lateral bud. Moreover, the spores rendered sterile by adverse conditions are shed from the sporangia. Thus not infrequently one finds greatly elongated strobili with a basal zone of empty gaping sporangia, surmounted by two or three whorls of empty microsporangia, then a zone of sprouting embryos, and an apical region of degenerating young stages of megasporangia. In contrast with this are the strobili which have developed under continuous favorable conditions, in which the *basal zone* displays embryos. Whether or not the strobilus may carry on its growth a third year in case of two successive failures to produce embryos, remains to be demonstrated. It will be a matter of interest to discover what variation in ecological conditions causes the strobili of the allied Texas species to pass the winter in a microsporangiate condition, whereas *S. rupestris* in Massachusetts appears to bear during the same season only megasporangia.

THE UNIVERSITY OF CHICAGO.

[*To be continued.*]

BRIEFER ARTICLES.

THE PROBABLE FUNCTION OF CALCIUM OXALATE CRYSTALS IN PLANTS.

A RATHER comprehensive study of vegetable histology (medicinal plants), extending over a period of six years, has brought to my attention more specifically the great abundance and wide distribution of crystals of calcium oxalate, and has led to the formulation of a theory as to their probable function in the plant economy.

There seems to be no logically deducible reason for assuming that the crystals serve as a protection against herbivorous animals, though such a theory was promulgated by Stahl and others and is now widely accepted by teachers of botany.

Calcium oxalate occurs in four predominating form types. Of these the least common is the crystal sand (Krystallsand, Krystallmehl, Krystallpulver) which occurs in the roots of belladonna, in the stem parenchyma of *Solanum dulcamara*, species of Atropa, Datura, Physalis; bark of Sambucus, Cinchona, and in some other plants. The prismatic and aggregate forms are perhaps about equally common and are very widely distributed. The needle-shaped or acicular crystals are also very common, but predominate in monocotyledonous plants.

Leaving out of consideration the still undecided question of the chemical formation of the crystals in the plant and the causes which lead to the production of one or the other form type, we shall refer briefly to their probable function.

G. Kraus in 1891 expressed it as his opinion that calcium oxalate was a reserve product to be redissolved by the plant and again utilized. This applies, however, only to a part of the crystals deposited during the previous season. Calcium oxalate dissolves with difficulty. It is insoluble in water, alcohol, ether, acetic acid, saliva, and other animal secretions. Being insoluble in these substances it is also tasteless; hence taste cannot enter as a factor to guard against destruction by herbivorous animals. Nor is this substance poisonous. Some of it would no doubt be decomposed by the secretions of the digestive tract (as free hydrochloric acid in the stomach), but not enough to produce poisoning due to

the oxalic acid liberated. It is generally admitted that the oxalic acid in various plants, as Rheum, Rumex, etc., serves as a protection against animals, not because of its highly poisonous nature, but because of the extremely sour and astringent taste.

The theory that calcium oxalate serves to keep away animals through mechanical interference is highly improbable for several reasons. If this were the case the crystals would be peripherally located, as in this position they would soonest produce the desired effect. The crystals actually occur about uniformly distributed through the tissues of the various plant organs, and are in many instances especially abundant in the interior, as in the spongy tissue of leaves, the pith of stems, and the heart wood of stems. This mechanical interference can have application to small animals only, such as snails, insect larvae, etc. The crystals could not possibly injure or repel large animals capable of destroying the entire plant rapidly.

Based upon observation, the conclusion is reached that the prime function of calcium oxalate in plants is that of mechanical support; secondarily it plays the part of a reserve product as stated by Kraus. The following are the chief reasons in favor of the mechanical support theory:

1. Cells containing prismatic crystals are quite generally associated with bast fibers. These crystal-bearing fibers consist of rows of rectangular, thin-walled cells, each cell bearing, as a rule, a single crystal. The cells surround the bast fibers or bast bundles. They are very abundant and distinct in the bark of Salix, Quercus, and Populus, for example. They enclose completely the single enormous bast cells of quebracho, and occur in the majority of bast-bearing barks and stems, and are associated with the bast tissue of vascular bundles. Bast cells are essentially non-elastic; the crystal-bearing cells and fibers enclosing the bast give elasticity. This is shown to a remarkable degree in the inner bark of Quillaja, which contains an enormous quantity of large, elongated prismatic crystals of calcium oxalate distributed through the bark parenchyma.

2. In other instances the crystal-bearing cells are not merely an aid to mechanical tissues, but serve as a substitute therefor, functionally taking the place of sclerenchyma. For example, in the seed of quince there is found a sclerenchymatous tissue below the layer of mucilaginous epidermal cells. In the white garden bean this sclerenchymatous tissue is replaced by a layer of cells carrying large prismatic

crystals so constructed and placed as best to resist vertical and diagonal pressure, as of soil particles and the weight of the bean.

In the case of acicular crystals, so prevalent in monocotyls, it is evident that they give elasticity as well as support against crushing pressure. This applies especially to the very long and comparatively thick needles of calcium oxalate found in squill, iris, and other members of the lily family. These crystals (raphides) are especially common in the parenchyma of roots, rhizomes, tuberous roots, stems, and leaves.

It is generally admitted that the cystoliths of Ficus leaves, etc., perform a purely mechanical function. In plant organs subjected principally to a radial pressure, as are thick roots, tubers, thick rhizomes, etc., not specially supplied with mechanical elements, the aggregate crystals predominate, *e. g.*, Rheum and Rumex. In such organs as potatoes, corms of Colchicum, etc., the necessary mechanical support is given by the starch which fills the cells. A potato free from starch would be crushed by the soil in which it grows.

Further evidence in favor of the mechanical support theory of calcium oxalate is to be deduced from the fact that in many instances the crystals are imbedded in a gelatinous or mucilaginous substance which equalizes the pressure exerted, acting as a bumper between cell-wall and crystal. In other instances the cell-sap takes the place of the mucilage.

It is very frequently found that cells bearing calcium oxalate take the place of mechanical cells in leaves. The crystals are especially common in the cells bounding the air chamber of stomata which certainly require some mechanical support.

It is also highly probable that calcium oxalate is merely accidentally present in some plants and plant organs, but in the majority of instances its presence points toward a function of mechanical support as indicated.— ALBERT SCHNEIDER, *Northwestern University School of Pharmacy, Chicago.*

CURRENT LITERATURE.

BOOK REVIEWS.

Perception and propagation of stimuli in roots.

A NEW FIELD of research in plant tropisms has recently been opened by Němec in two important papers dealing with the normal and pathological cytology of the cells of sensitive and curving regions of roots and stems. In the first of these[1] the author shows that there exist starch grains in the cells of the root caps of many roots, and in several other sensitive regions. These grains invariably occupy the physically lower side of the cells in which the lie. Most of the experiments were conducted upon the roots of seedlings and upon the coleoptiles of grasses. At the close of an experiment the organs were killed, and studied by staining and sectioning. The movement of the grains occupies a comparatively short time, a half hour being sufficient for their rearrangement in the cells of the root cap in Pisum, when this has been turned on one side. The grains are embedded in the plasma, and as they fall away from that part of the protoplasm against which they normally lie (*i. e.*, when the organ is upright), the protoplasm on that side of the cell becomes altered so that it stains much more deeply. If the organ has been so placed that when the grains come to rest they still lie against a part of the normally lower wall, only that part of the protoplasm which has been freed from them becomes altered. Cells which have been in an upright position, but have lost their starch, owing to the influence of a plaster jacket, show the same proptoplasmic thickening as those which have been turned so that the grains fall by gravitation away from their normal position. Roots so treated are found to have lost their power of geotropic curvature. The author suggests that this may be due to the loss of the starch. Also, when these roots are freed from the plaster and allowed to renew their growth, they regain their normal sensitiveness. The return of sensitiveness is accompanied by the formation of new starch grains in the root cap. Also, if the region containing the grains be cut away, geotropic reaction ceases for a time, and its return is simultaneous with the formation of new grains in the regenerated tissue.

Němec is of the opinion that the stimulus for geotropic curvature is the change of pressure of the starch grains upon the protoplasm. These variations in pressure are of such small magnitude, however, that it is well-nigh

[1] NĚMEC, B.: Ueber die Wahrnehmung des Schwerkraftreizes bei den Pflanzen. Jahrb. f. wiss. Bot. 36: 80–178. 1901.

inconceivable that they should produce an effect great enough to be propagated through many cells and produce a reaction. It seems much more probable to us that the sensitiveness is due rather to a chemical than to a physical change of condition within the cells. This seems the more probable on account of the fact that when the grains leave their normal position, the protoplasm here becomes changed. Possibly this may be due to the removal, not of the grain, but of the leucoplast in connection with it. The chemical effect of the leucoplast upon sugars passing through it is very great (since it produces in them condensation to form starch), and it may well be that it also has an effect upon the surrounding protoplasm. There may be other, as yet invisible, substances within the cell, which cannot diffuse readily, whose specific gravity differs from that of the protoplasm, and these might affect the protoplasm unsymmetrically, thus setting up a stimulus which could be propagated to the curving region.

The second paper[2] treats of the conduction of the stimulus from the sensitive regions to the region of the curvature. Traumatropic responses in roots were chosen as field for experimentation. If the tip of an Allium root is wounded by a cut or needle thrust, the protoplasm of the meristematic cells bordering upon the wound heaps up and becomes more dense on the side toward the wound. The nucleus also migrates toward the wound, often coming to lie against the wall on that side of the cell. After a very short time these cells regain their normal condition. But in the meantime a second and third layer of cells, at the side of and behind the wound, have responded in the same manner. Thus in roots killed 15 minutes after wounding, the response has been propagated through 1.25 mm of tissue, but those cells within 1 mm of the wound have already regained their original condition. This propagation takes place most rapidly in a longitudinal direction, but only towards the base of the root. It also occurs in both directions laterally.

A careful investigation was made to determine whether this difference in the rate of propagation of the response might correspond to any difference in structure. In the cells taking part in the traumatropic reaction, longitudinal strands of protoplasm can, by proper staining, be made visible with comparatively low magnification. Sometimes there is a single strand, sometimes several; sometimes they lie near the middle of the cell, and sometimes, especially in vacuolated cells, along the lateral walls. The strands are always in contact with the nucleus, often dividing and enclosing this body between several branches which reunite beyond it. A differential stain for the branches has not been discovered, but they take the ordinary stains much more deeply than the surrounding protoplasm. The best results were obtained by staining strongly with fuchsin S.

[2] NĚMEC, B.: Die Reizleitung und die reizleitenden Strukturen bei den Pflanzen. 8vo. pp. iv + 154. *pls. 3. figs. 10.* Jena: Gustav Fischer. 1901. Cf. note BOT. GAZ. 31: 133. 1901.

By use of high magnification the protoplasmic strands in Allium root tips can be shown to be bundles of fibrillae. These fibrillae have a definite sheath and lie embedded in a special plasma. In other plants the fibrillae could not be so well made out, but enough was accomplished to convince the author that, in general, the longitudinal strands are fascicles of smaller fibrils. In longitudinally adjacent cells the strands (and in Allium, at least the fibrillae also) correspond on the opposite side of cross walls, and the author supposes that the fibrillae are in contact, or perhaps continuous, through these walls. Transverse fibrils were found in certain cells, but never in bundles.

The question whether or not these fibrillae have any connection with the transmission of traumatropic and other stimuli is a difficult one to answer. The influence of a number of changes in external conditions was determined, first with regard to the propagation of the traumatropic reaction, and then with regard to the fibrils. It was found that the conditions which cause a degeneration of the fibrillae diminish the rate of propagation or cause this phenomenon to cease altogether. By a sudden change in temperature the fibrils may be caused to degenerate, but later (unless the change is too great) they form again. The same change lessens the rate of, or puts an end to, propagation of the traumatropic response in the longitudinal direction, but after a time the cells regain their power to respond normally. The return of this power to the cells is always accompanied by the regeneration of the fibrillae.

Another line of evidence is furnished by the study of certain roots of Allium which exhibited an apparently spontaneous nutation, uninfluenced by gravity. In these the starch-bearing cells of the root cap were perfectly normal in appearance and behavior, but in almost all of these roots the bundles of fibrillae were disorganized. Still other evidence was obtained from *Vicia faba*. In roots of this plant the fibrillae are found only in the large plerome cells. If the plerome is severed by a knife-thrust the geotropic reaction either occurs not at all, or bending takes place only so far up the root as the wound. Němec concludes that the bundles of fibrils are the path of conduction for traumatropic, geotropic, and other stimuli. The fibrils are strands of protoplasm specialized for conduction.

The two pieces of research here reviewed are accompanied by figures which are certainly convincing with regard to the facts. To us it appears that the conclusions of the second paper are much better supported by experiment than those of the first. The bundles surely bear a close relation to the process of conduction, whether this relation be causal or not. The author compares the fibrils to the nerve fibers of animals, but it seems to us that there is little similarity.—BURTON EDWARD LIVINGSTON.

Two new books on plant physiology.[3]

THE dearth of text-books on plant physiology seems about at an end. We record with pleasure the almost simultaneous publication of two books on this subject, one by Professor D. T. MacDougal, of the New York Botanical Garden, the other by Professor W. F. Ganong, of Smith College. It is significant that both these books are American.

The first named volume comprises a very comprehensive, though necessarily brief, account of the phenomena of plant physiology, together with explicit directions for laboratory experimentation. Discussion of principles and laboratory directions are so interwoven that the temptation for the student to work mechanically, without other end in view than to finish the experiment, must here be reduced to a minimum. For this reason the book may be found more useful on the laboratory table than in the reading room. The mere reader will often be disappointed by the absence of measurements, etc., since it is intended that these shall be obtained in the laboratory. On the other hand, it will be well-nigh impossible for one to peruse any section without gaining a fair knowledge of the methods by which the principles there treated are established.

After an introductory chapter on the nature and relations of an organism (in which many statements are unavoidably made which the student cannot understand until he has gone further) the author devotes seven chapters to the presentation of the subject of irritability. In each of these a group of external conditions and the influence of these upon the plant is taken up. These chapters are headed as follows: Relations of plants to mechanical forces, Influence of chemicals upon plants, Relation of plants to water, Relation of plants to gravitation, Relation of plants to temperature, Relation of plants to electricity and other forms of energy (although there are no "other forms" mentioned here), and Relations of plants to light. The chapter on the influence of chemicals will be found especially valuable. The next chapter (IX) deals with the composition of the body, and consists of a very brief treatment of the different groups of compounds found in the plant, followed by methods for their extraction, separation, and identification. This discussion is so brief that the reader may be led into error by generalizations; and students will need to be cautioned that the qualifying phrases in the chapter are very important.

Following this are five chapters on the processes going on within the living plant. These are entitled: Exchange and movements of fluids, Nutritive metabolism, Respiration, Fermentation and digestion, Growth, and

[3] MACDOUGAL, D. T.: Practical text-book of plant physiology. 8vo. pp. xiv + 352. *figs. 159*. New York: Longmans, Green & Co., 1901.

GANONG, W. F.: A laboratory course in plant physiology, especially as a basis for ecology. 8vo. pp. vi + 147. *figs. 35*. New York: Henry Holt & Co., 1901.

Reproduction. The treatment of enzymes, which have become so important a consideration within the last few years, is comparatively full, both in the chapter on the composition of the plant and in that on nutrition, and will be especially useful.

Following the chapters on processes within the plant, the last chapter in the book gives a very excellent exposition of the subject of vegetative propagation throughout the plant kingdom. Sexual reproduction is not treated. At the end is a valuable appendix containing tables of physical constants, such as the expansion of air at different temperatures from 0° to 35°, the density of oxygen and of carbon dioxid, the absorption of these gases by water, etc. It will be a great aid, in experiments where calculation is necessary, to have these tables in a convenient form for reference.

Regarding the style, we wish it might have been clearer in places; there will surely arise difficulties of interpretation now and then. The only important point of theory wherein the author may find others in disagreement with him is that which expresses itself here and there in the idea of some *purpose* underlying the whole field of plant phenomena. For instance, it is stated that there exist "reactions to shock . . . . which the most thorough investigation has failed to invest with a purpose. New relations of the plant may be discovered, however, which will interpret these reactions."

The book is fully illustrated throughout, including many figures of apparatus. References to the most important recent publications on the different topics are given as footnotes, and both treatment and references are surprisingly up to date, articles being cited which appeared only a few months ago. The index is complete, and includes footnotes as well as text. The arrangement of the subject-matter is thoroughly scientific, which fact, together with its general completeness and reliability, should give the book a broad and constant use in laboratories where the subject is taught.

Professor Ganong's new book does not attempt to present any general discussion of the subject, but is designed, as its title denotes, for laboratory use only. It is divided into two parts, the first being on methods of study and necessary equipment, while the second comprises the true outline of the course. Part I is written largely for the teacher, and every teacher of laboratory science (whether it be physiology or not) will do well to read it. The first two sections of this part are especially noteworthy for their fund of pedagogical ideas, which, it seems to us, are almost all philosophically and practically sound. The third and fourth sections deal with laboratory, greenhouse, and materials for the course. Section 5 gives practical directions for a great number of laboratory manipulations, some of which often are a source of considerable trouble to the inexperienced. This will surely prove a very valuable part of the book.

Part II, the outline of the course itself, consists of two divisions. Division

I treats of the structure and properties of protoplasm, including its composition, its relation to external conditions, and its power of organism building. Division II deals with the physiological operations of plants. Here are included nutrition, growth, reproduction, irritability, locomotion, and protection. The last two are not treated, however, the statement being made that they are almost purely ecological in their nature.

The titles of the exercises throughout this entire part are put in the form of questions. The directions which follow are designed to aid the student in answering the question, but do not answer it for him. Just enough discussion is brought in with the laboratory directions to arouse the student's interest in the experiment in hand, and to make him appreciate what are its essential points. Ample references to the literature are constantly given, even to original articles; the author believes that direct contact with the sources of information is of great pedagogical value. Good half-tone reproductions of photographs show the student just how the more complicated forms of apparatus are to be set up. With their aid he should be able to bring his experiment to completion with a minimum amount of aid from the teacher.

Following this part are several pages of addenda in which are noted numerous improvements upon apparatus described in the body of the book.

The course as outlined by Professor Ganong will doubtless occupy more time than many can give to an elementary course in plant physiology. For such teachers the book will still be useful, since it is so well arranged that one can easily strike out a topic here and there without materially affecting the course as a whole. The style is clear, vivid, and scholarly throughout. We can think of no book yet published which might better "serve as a guide to the acquisition of a general physiological education."—BURTON EDWARD LIVINGSTON.

MINOR NOTICES.

THE *Transactions* of the American Microscopical Society **21**: 1900, contains 275 pages devoted largely to zoological papers and matters of general interest. The following are of special interest to botanists: C. A. KOFOID, *The plankton of Echo river, Mammoth cave;* HENRY B. WARD, *Comparative study of methods in plankton measurements;* GEORGE C. WHIPPLE, *Chlamydomonas and its effect on water supplies;* CHARLES E. BESSEY, *The modern conception of the structure and classification of diatoms,* with a division of the tribes and a rearrangement of the North American genera. Professor Bessey accepts Müller's view that the filamentous condition is the primitive one, and that diatoms should be regarded as typically filamentous rather than as unicellular forms. They should then be classed between the Peridiniales on the one hand, and the Desmidiaceae and Zygnemaceae on the other. The Zygnemaceae are regarded as the most primitive

of the Conjugatae, while the desmids and diatoms are believed to represent two similar and somewhat parallel genetic lines in which the filaments tend to break up rather early into independent cells. The larger part of the paper is occupied by a key to the tribes and genera of the American forms.— CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS

EXPERIMENTS by D. Neljubow[4] have shown that the peculiar horizontal nutation of stems of seedling peas (*Pisum sativum*) grown in darkness at high temperature is due to the presence of small amounts of illuminating gas in the air of the laboratory. It is especially the acetylene and ethylene components of illuminating gas which are active. SO_2, and vapors of CS_2, xylol, and benzol are very injurious. This peculiar reaction to gas seems to have been unknown before.— C. R. B.

A FEW interesting points regarding the behavior of apples in cold storage are brought out in a bulletin[5] by L. C. Corbett on this subject. With the exception of York Imperial, the apples of all varieties tested lost less in weight when stored in the light than when kept in darkness. The acid content of the apples was markedly decreased during storage, while the sugar content was decreased in some varieties and increased in others. No explanation for these differences of behavior is attempted.— ERNST A. BESSEY.

A NUMBER of experiments throwing light on the method of infection in pear blight are described in a bulletin[6] from the Delaware Experiment Station. The germs were introduced by means of needle punctures into terminal shoots, one year old wood, three year old wood, buds, leaves, and fruit. Leaves and young twigs were smeared with cultures of the germ and kept moist for a time. The latter, however did not cause the disease to develop, for it appeared only where the germs had actually been introduced into the tissue, as for example, where needle punctures had been made into the present year's terminal shoots, into buds, leaves, and into the fruit. The punctures into three-year old wood produced only small diseased areas. The author's conclusions are that pear blight is only communicated, as pointed out by Waite, by transference of the germs by honey-seeking insects from nectary to nectary, and into the fruits, young succulent shoots, and leaves by the introduction through bites and punctures of insects of germs clinging to their mouth parts. The same bulletin reports the occurrence in Delaware of pear canker, which seems to be caused by *Sphaeropsis malorum*.

[4] Beihefte z. Bot. Cent. **10**: 128–138. *figs. 2.* 1901.

[5] CORBETT, L. C.: Cold storage. Bull. West Virginia Agr. Expt. Sta. 74: 51–80. *figs. 1–3.* March 1901. Morgantown.

[6] CHESTER, F. D.: Pear blight and pear canker. Bull. Delaware Agr. Expt. Sta. 52: 1–8. *figs. 1–7.* April 1901. Newark.

Spraying with Bordeaux mixture is recommended as a preventive measure for this disease.— ERNST A. BESSEY.

DR. BRADLEY M. DAVIS has recently published[7] some interesting studies on the nucleus of Pellia. These studies were undertaken with the object of extending our knowledge of the cytology of the Hepaticae, and with the hope of throwing some light on the relationships of the various morphological manifestations of kinoplasm. To accomplish this three phases in the life history of the plant were examined, namely sporogenesis, the germination of the spore, and the vegetative activities in the seta. In the spore mother cell the spindles are organized in the same manner as that characteristic of the pteridophytes and spermatophytes. In the stages of spore germination asters with centrospheres were found during the prophase. These appear to be transitory structures, however, as they disappear before the daughter nuclei are formed. In the vegetative cells the spindles are formed in essentially the same fashion as that described by Hof and Němec for the vegetative cells of many spermatophytes. The kinoplasm here forms two caps fitting closely over the ends of the nucleus which has become elongated, and these caps are changed into the poles of the spindle. The writer concludes, however, that the kinoplasmic fibrillae, the centrospheres, and kinoplasmic caps are all secondary developments from the primal granular protoplasm which is the only form of kinoplasm in any sense permanent in the cell. The paper forms an extremely interesting contribution and contains much that is of importance on the cytology of the Hepaticae.—A. A. LAWSON.

CENTROSOMES in flowering plants are described by Bernard[8] in a series of short papers. From a study of *Lilium candidum*, *L. Martagon* and *Helosis Guayanensis* the writer convinced himself of the presence of the much discussed structures. Material was fixed in alcohol and in Flemming's solution and was stained in a mixture of fuchsin and iodine green (1 per cent. aqueous solution of fuchsin, 2 parts; 1 per cent. aqueous solution of iodin green, 2 parts and water 40 parts). The safranin gentian-violet orange combination did not give as good results.

In *L. candidum* the centrosomes were found quite regularly during various phases in the germination of the megaspore. They resemble the structures described by Guignard, but are not so sharply defined. The centrosome was also identified in the gametophytes of Helosis. In *L. Martagon* centrosomes were found in the female gametophyte, in the vegetative cells of the ovule, but could not be positively identified in the endosperm. The centrosome is cytoplasmic in origin.

[7] Nuclear studies on Pellia. Ann. Bot. **15**: 147–180. *pls. 10–11*. 1901.

[8] BERNARD, C. H.: Recherches sur les sphères attractives chez *Lilium candidum*, *Helosis Guayanensis*, etc. Jour. de Botanique **14**: 118–124, 177–188, 206–212. *pls. 4–5*. 1900.

Incidentally, it is noted that there are sometimes two embryo sacs in *L. candidum*. In these species a very large vacuole develops between the two polar nuclei preventing the nuclei from fusing. The writer suggests that this may account for the sterility of this species. It is also noted that the upper polar nucleus and the nuclei of the egg and synergids are erythrophilous, while the four nuclei at the antipodal end of the sac are cyanophilous. This difference in chromatophily is attributed to chemical differences due to sexuality, the nuclei at the antipodal end of the sac having lost all sexual character.—CHARLES J. CHAMBERLAIN.

ITEMS OF TAXONOMIC INTEREST are as follows: H. J. BANKER (Bull. Torr. Bot. Club **28**: 199–222. 1901) has published a synopsis of the species of Hydnum, 40 being recognized, and one described as new.—AVEN NELSON (*idem* 223–235), in his 13th paper entitled "New plants from Wyoming," has described 18 new species and varieties belonging to various families.—DAVID GRIFFITHS (*idem* 236–241) has described a new ergot growing on species of Hilaria in Arizona.—MAXWELL T. MASTERS (Bot. Jahrb. Beibl. **29**: no. 66. pts. 3–4. 1–20. D1900) has published numerous new species of Restionaceae from the Cape of Good Hope, including a new genus (*Phyllocomos*).—H. CHRIST (Bull. Herb. Boiss. II. **1**: 445–460. 1901) has published a number of new species of ferns from Dutch New Guinea.—In Torreya (1:41–43. 1901) N. L. BRITTON has described a new Hieracium from Florida, E. L. GREENE a new Arnica from Oregon, and W. J. BEAL a new Panicularia from Colorado.—B. SHIMEK (Bull. Lab. Nat. Hist. Iowa Univ. **5**: 139–170. 1901) has published a list of the pteridophytes of Iowa, with stations.—T. MAKINO and K. SHIBATA (Bot. Mag. Tokyo **15**: 1-14. *pl. 1.* 1901) have described a new genus (*Sasa*) of Bambuseae, including eight species which have heretofore been referred to Bambusa. The name is a common Japanese name for "small bamboos."—Among some recently published notes on algae (Zoe **5**: 121–129. 1901) W. A. SETCHELL has described new genera as follows: *Hedophyllum* and *Pleurophycus* (both Laminariaceae), and *Weeksia* (Dumontiaceae).—B. L. ROBINSON (Proc. Am. Acad. **36**: 455–488. 1901), in a recent Contribution from the Gray Herbarium, has published as follows: A synopsis of the genus Melampodium, 36 species being recognized, 7 of which are new; a synopsis of the genus Nocca (Lagascea), 14 species being recognized, 3 of which are new; new species and newly noted synonymy among the spermatophytes of Mexico and Central America, the genus Eupatorium receiving 15 new species.—M. L. FERNALD (*idem* 491–506) has described a fascicle of new seed-plants from Mexico and Central America. Among them is a new genus of Euphorbiaceae (Hippomaneae), *Alcoceria* by name.—WILLIAM TRELEASE (Rept. Mo. Bot. Gard. **12**: 79–80. *pls. 35–37*. 1901) has published a new palmetto (*Sabal Uresana*) from Sonora.—J. M. C.

NEWS.

PROFESSOR MAXIME CORNU, of the Jardin des Plantes, Paris, died on April 3, in the fifty-ninth year of his age.

DR. DUNCAN S. JOHNSON, associate in botany at Johns Hopkins University, has been promoted to an associate professorship.

DR. ALEXANDER P. ANDERSON has been appointed assistant in botany in Columbia University to succeed Dr. M. A. Howe. Dr. Anderson will also carry on physiological studies at the New York Botanical Garden.

MR. GEORGE P. CLINTON, of the botanical department of the University of Illinois, spent last year at Harvard University on leave of absence. His leave has been extended for another year. He is at work upon the Ustilagineae.

DR. MARSHALL A. HOWE has been appointed assistant in the New York Botanical Garden and will devote himself especially to the study of the red algae. He is spending the summer in the eastern provinces of Nova Scotia, Cape Breton, and Newfoundland.

FROM *Science* we learn that Dr. H. W. Harkness, well known as a botanist of the Pacific coast, and especially for his recent studies on the Tuberaceae, died in San Francisco on May 10. His collections become the property of the California Academy of Sciences.

DR. F. L. STEVENS, who has spent the past year in Europe as an honorary fellow of the University of Chicago, has been appointed instructor in biology at the College of Agriculture and Mechanic Arts, Raleigh, North Carolina. He will have entire charge of the newly-established department.

DR. L. M. UNDERWOOD spent the months of June and July in botanical exploration in Porto Rico in connection with a party from the Department of Agriculture at Washington, consisting of O. F. Cook, special agent for tropical agriculture, Guy N. Collins, plant photographer, and Robert F. Griggs, botanical collector.

MR. H. HASSELBRING, a graduate of Cornell University and later assistant in botany at the New York Agricultural Experiment Station, Geneva, has been appointed assistant in botany in the Agricultural Experiment Station of the University of Illinois. Mr. Hasselbring will devote his attention chiefly to plant pathology.

CHARLES F. HOTTES, Ph.D., formerly an assistant in the botanical laboratory of the University of Illinois, has just returned from three years study

at the University of Bonn. He is now promoted to an instructorship in botany, and is given charge of vegetable physiology. While abroad he gave chief attention to plant physiology and cytology. Some researches will be published shortly.

THE OPENING of the Minnesota Seaside Station at Point Renfrew, Vancouver island, took place June 21. Thirty students are in attendance. Evening lectures have been given by Miss Eloise Butler, of Minneapolis, Mr. K. Yendo, of the University of Tokio, Professor Conway MacMillan and Mr. Harold Lyon, of the University of Minnesota, and Professor Francis Ramaley, of the University of Colorado. The shore is exceedingly rich both in fauna and flora, and large collections are being made by some members of the party.

IN THE department of botany of the University of California Dr. W. J. V. Osterhout has been promoted to an assistant professorship. Professor W. L. Jepson is this summer exploring the western portion of the Colorado desert about San Jacinto mountain, in company with Mr. H. M. Hall, assistant in the herbarium. They will also make an exploration in Humboldt and Del Norte counties. Mr. N. L. Gardner, assistant, is making further studies of the algae of the Puget sound region. Dr. W. A. Setchell is at Pacific Grove, California, investigating the ecology and zonal distribution of the marine algae.

BOTANISTS will be interested in the organization of the new Bureau of Plant Industry of United States Department of Agriculture. The old divisional lines have been eliminated and instead the work has been divided into various related groups, as follows: Vegetable pathological and physiological investigations; Botanical investigations and experiments: Pomological investigations; Grass and forage plant investigations; Experimental gardens and grounds; Arlington experimental farm; Congressional seed distribution; Seed and plant introduction; and Tea culture experiments. The executive officers of the bureau are:

Beverly T. Galloway, physiologist and pathologist, and chief of bureau.

Albert F. Woods, pathologist and physiologist in charge of vegetable pathological and physiological investigations, and acting chief of the bureau in the absence of the chief.

Frederick V. Coville, botanist, in charge of botanical investigations and experiments.

F. Lamson-Scribner, agrostologist, in charge of grass and forage plant investigations.

Gustavus B. Brackett, pomologist, in charge of pomological investigations.

The pathological investigations are conducted by the following staff: Erwin F. Smith, pathologist, in charge of laboratory of plant pathology; Walter T. Swingle, physiologist, in charge of laboratory of plant physiology;

Herbert J. Webber, physiologist, in charge of laboratory of plant breeding; Newton B. Pierce, pathologist, in charge of Pacific coast laboratory; Hermann von Schrenk, special agent, in charge of Mississippi valley laboratory; Peter H. Rolfs, pathologist, in charge of tropical laboratory; Merton B. Waite, assistant pathologist, diseases of orchard fruits; Mark Alfred Carleton, cerealist; C. O. Townsend, pathologist; George T. Moore, physiologist; B. M. Duggar, physiologist; Rodney H. True, physiologist; William A. Orton, assistant pathologist; Joseph H. Chamberlain, expert in physiological chemistry; Thomas H. Kearney, assistant physiologist; Cornelius F. Shear, assistant pathologist; Flora W. Patterson, mycologist.

The botanical investigations and experiments are conducted by the following staff: O. F. Cook, botanist, in charge of tropical agriculture; A. J. Pieters, botanist, in charge of seed testing laboratory; V. K. Chestnut, botanist, in charge of investigations of poisonous weeds; Lyster F. Dewey, assistant botanist; Carl S. Schofield, expert on cereals.

The following have charge of the grass and forage plant investigations: A. S. Hitchcock, assistant agrostologist, in charge of field work; David Griffiths, assistant agrostologist, in charge of field management; Elmer D. Merrill, assistant agrostologist, in charge of collections; C. R. Ball, assistant agrostologist.

The officers of the pomological investigations are: William A. Taylor, pomologist, in charge of field investigations; H. P. Gould, pomologist, in charge of fruit district investigations; George C. Husmann, expert, in charge of grape investigations.

The following branches are conducted under the direction of the chief of the bureau, but the officers directly in charge are given under each branch:

Experimental Gardens and Grounds: L. C. Corbett, hoticulturist; E. M. Byrnes, head gardener; George W. Oliver, expert plant propagator.

Congressional Seed Distribution: Robert J. Whittleton, superintendent of weighing and mailing section; James Morrison, superintendent of records.

Seed and Plant Introduction: Ernst A. Bessey, assistant in charge; David G. Fairchild, permanent agricultural explorer.

Arlington Experimental Farm: L. C. Corbett, horticulturist, in charge.

Tea Culture Experiments: Dr. Charles U. Shepard, in charge.